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Environmental drivers of spatiotemporal variation in the movement, performance, and genetic structure of brown trout and Atlantic salmon

Thesis presented by

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For the degree of

Doctor of Philosophy

University College Cork

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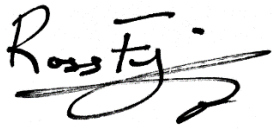
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Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism.



Ross W. Finlay

Abstract

Environmental conditions vary spatially and temporally, providing organisms with both challenges and opportunities. Animals have evolved a spectacular variety of migratory behaviours to take advantage of environmental variation, encompassing movements that are conducted in anticipation of predictable variation as well as movements undertaken in reaction to more stochastic variation. The spatiotemporal pattern of migratory movements displayed by a population or species can be thought of as the evolutionary outcome of trade-offs amongst life history traits. As such, the study of animal movement in relation to environmental heterogeneity can yield valuable insights into the proximate and ultimate drivers of migratory behaviours as well as the behavioural mechanisms underpinning genetic structure. Against this background, the overarching aim of this thesis is to investigate the role of environmental heterogeneity in shaping locally-adapted migratory behaviours, fine-scale genetic structure and physiological performance in populations of wild brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*).

Using telemetry data from passive integrated transponder (PIT) tags, I investigated the fine scale spatiotemporal patterns of spawning-related movements of brown trout between a feeding lake and two spawning streams (one inflowing, one outflowing, separated by < 100 m) over two spawning seasons. The timing of seasonal, daily and diel movements was strongly associated with variation in photoperiod, stream height and moon phase. Movement activity was highest at night, and particularly on nights with minimal lunar illumination and high water levels, suggesting that trout synchronise their spawning movements with environmental conditions that minimise their visibility to predators. Males began their movements between the lake and

streams significantly earlier in the spawning season than females (protandry) and were generally more active.

A substantial proportion of trout entered both spawning streams during the spawning periods, providing potential sources of gene flow between the two streams. However, Bayesian analyses revealed the existence of subtle genetic differentiation between juvenile trout sampled in the two streams and indicated that gene flow was strongly asymmetrical in a predominantly downstream (i.e. inflow to outflow) direction. Thus, natal dispersal between the two streams appears to be more common amongst trout that hatch in the inflow than the outflow. These findings have important implications for genetic diversity and local adaptation of fish stocks in fluvial and lacustrine environments.

The collection of PIT-derived data in fluvial habitats is often hindered by the fragility of PIT antennae when exposed to high flows and flotsam. In Chapter 3 I present a novel PIT antenna design I developed for use in flood-prone spatey rivers. This design allows flotsam to pass without causing significant damage to antennae and was crucial for collecting the data used in Chapters 4 and 5 and in Appendix A.

The performance of migratory populations can be strongly influenced by factors that affect the physiology or survival of migrants in any encountered habitat. I therefore investigated whether the acanthocephalan endoparasite *Pomphorhynchus laevis* causes a habitat-specific (i.e. freshwater or saltwater) pathology in Atlantic salmon smolts. Peculiarly for the species, the Irish strain of *P. laevis* uses salmonids, instead of cyprinids, as its preferred definitive hosts. Despite observing high prevalence of the parasite amongst wild smolts and high infection intensities in some individuals, I found no evidence of a pathological effect of infection in fresh or salt water.

However, I did demonstrate that this freshwater parasite can survive in smolts in salinities similar to those found in coastal waters for at least 72 hours. Thus, the coastal roaming behaviour of Irish sea trout may have facilitated the colonisation of Irish river systems, resulting in the exceptionally widespread distribution of the parasite in Ireland.

Collectively, these results contribute to our knowledge of how environmental heterogeneity influences the movement, performance, distribution and genetic structure of organisms in aquatic environments. As modern environmental changes occur at an unprecedented pace, such knowledge may provide us with the ability to anticipate, and perhaps even ameliorate, the impacts that anthropogenic activities have on migratory species.

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Finally, I want to thank Kat. Without your patience, humour, positivity and support I could never have gotten this far. Thank you for everything. I look forward to a lifetime of adventures with you.

I dedicate this work to my daughter, who is due to arrive in this world very, very soon. I can't wait to meet you!

Chapter 1

General introduction

Movement, in one form or another, is a ubiquitous and defining feature of animal life. As such, movement ecology and, in particular, the study of animal migration, encompasses an incredible variety of behaviours conducted over a vast range of spatial and temporal scales. From the Adélie penguin (*Pygoscelis adeliae*) that annually crosses thousands of kilometres of open ocean between feeding grounds and nursery habitats, to zooplankton that descend tens of meters through the water column as the first light of each day illuminates the surface and exposes them to predators, migratory behaviour amongst animal taxa is driven by a diverse range of proximate and ultimate causes (Davis, Boersma and Court, 1996; Lampart, 1989; Lack, 1968). What constitutes animal migration is a matter of some debate, with numerous definitions in the literature (Hansson and Åkesson, 2014). For the purposes of this thesis I have used the following definition: The movement of animals between two distinct habitats on a reasonably predictable temporal basis.

Fundamentally, migration allows individuals to increase their fitness by exploiting spatiotemporal variation in resources, environmental conditions and mortality risks (Chapman et al., 2014; Lucas et al., 2001; Abrahms et al., 2019). Although animal movement can be directly motivated by deteriorating conditions in the origin habitat (Lack, 1968), the evolved migratory behaviours of many species may be thought of as anticipatory in the sense that migrants move between habitats at a time when the long-term average conditions in the destination habitat have been favourable for a particular activity and the risks associated with movement between habitats have

generally been tolerable (Shaw, 2016; Forrest and Miller-Rushing, 2010). Migratory species use an assortment of environmental variables such as photoperiod, temperature, ocean currents, and Earth's magnetic field as signals in order to decide when and where to migrate, and how to accomplish the journey (Cochran, Mouritsen and Wikelski, 2004; Cresci et al., 2019; Dittman and Quinn, 1996; Gwinner, 1989; Haraldstad et al., 2016). However, reliance on multiple habitats with predictable temporal heterogeneity in conditions or resources has made migratory species particularly vulnerable to the ill-effects of anthropogenic activities (Wilcove, 2008; Seebacher and Post, 2015). Habitat fragmentation and the creation of physical barriers can directly prevent movement between habitats while increased migrant mortality (through the overexploitation of migrants or altered dynamics between migrants, prey, predators and parasites) can alter the historical balance between the fitness benefits and costs of migration itself and threaten population persistence amongst obligate migrants (Shaw, 2016). Furthermore, as habitats become degraded and climate change causes seasonal environmental conditions to decouple from long-term seasonal patterns, evolved responses to environmental cues may deliver migrants to sub-optimal locations at sub-optimal times (Cushing, 1990). Thus, migrants are increasingly likely to encounter unfavourable conditions in destination habitats or during their migratory movements (Lennox et al., 2016; Abrahms et al., 2019; Scranton and Amarasekare, 2017). Indeed, many of the world's most spectacular migrations have already disappeared as a result of human activities (Wilcove and Wikelski, 2008), while modern declines in populations of European-breeding long-distance migratory birds have been more sustained and more severe than in their non-migratory counterparts (Sanderson et al., 2006).

Against this background, identification of the proximate and ultimate drivers of movement behaviour will play a crucial role in allowing us to predict the impacts of climate change and human activities on the performance and phenology of migratory populations. In addition, spatial patterns of dispersal and gene flow, in conjunction with the grain of environmental variation, influence spatial patterns of local adaptation (Kawecki and Ebert, 2004; Kawecki and Holt, 2002; Fedorka et al., 2012). Patterns of local adaptation, in turn, can influence spatial patterns of neutral genetic differentiation among populations (population structure) via isolation-by-adaptation processes (Quinn, Unwin and Kinnison, 2000; Nosil, Egan and Funk, 2008; Orsini et al., 2013). Genetic and phenotypic differentiation among populations, in turn, provides demographic stability at the stock or meta-population level via portfolio effects (Schindler, Armstrong and Reed, 2015). As such, an understanding of the geographic scales at which migratory populations are structured (including associated gene flow patterns), as well as the behavioural basis of such genetic structure, should underpin management strategies and, in particular, the designation of management units (Carlsson et al., 1999). Furthermore, because the maintenance of genetic diversity is a key factor in determining the ability of species to adapt to and withstand environmental changes (Schindler, 2019; Reed et al., 2011), an appreciation of the evolutionary and ecological (including behavioural) processes underpinning the maintenance of diversity within and among populations is critical to wildlife management and conservation. Finally, if we are to develop informed and effective strategies for the conservation of migratory species we must identify causes of migrant mortality at each phase of the migrant's journey. This thesis contributes to these areas of knowledge using two species that display a range

of different migratory strategies, the Atlantic salmon (*Salmo salar* L.) and the brown trout (*S. trutta* L.), as case study animals.

Overview of life history patterns in Atlantic salmon and brown trout

Whether we are ecologists or anglers, geneticists or conservationists, teachers or children, it is hard not to be inspired by the iconic image of a leaping Atlantic salmon and the knowledge that the animal we observe has journeyed through thousands of kilometres of open ocean before returning to breed in the very stream it is likely to have originated from. While brown trout are often dismissed as a less charismatic cousin of the salmon, their remarkable phenotypic variability and diversity of enigmatic behaviours make them a constant source of curiosity for those more intimately acquainted with the species (Ferguson et al., 2019; Kent, 1990; Plunket-Greene, 1924; Sawyer, 1970). Both salmonids, along with their more distant relatives the Pacific salmonids, feature in folklore and literature throughout their native ranges and provide sustenance to millions of humans annually (Muhlfeld et al., 2019). In addition to their significant cultural, recreational, nutritional and economic value, these species play important roles in ecosystem functioning and as indicators of ecosystem vitality (Haak and Williams, 2013). While both Atlantic salmon and brown trout exhibit broad and divergent varieties of life history strategies, their shared ability to migrate between, and adapt to, differing habitats has been instrumental in their long-term successes (Ferguson et al., 2019; McGinnity et al., 2009; Nevoux et al., 2019; Jonsson and Jonsson, 2006).

The life-cycle of Atlantic salmon and brown trout begins and culminates in freshwater gravel beds where the movement of cool, well-oxygenated water provides

the necessary conditions for embryo development (Buffington, Montgomery, & Greenberg, 2004; Gauthey et al., 2015; Jonsson and Jonsson, 2011). These spawning areas are usually restricted to streams and rivers although salmonids will sometimes spawn in lakes if hydrological conditions and substrate composition are suitable (Penlington, 1983; Arostegui and Quinn, 2019). However, the availability of food and territory in fluvial habitats is typically restricted, thereby imposing density-dependent and density-independent constraints on individual growth and, ultimately, population size (De Eyto et al., 2016; Jonsson et al., 1998). Thus, feeding migrations represent a common life-history pathway for both species, allowing individuals to move from their natal streams and rivers to more productive and less confined habitats, where growth can be maintained and competition for territory is less severe (Marco-Rius et al., 2013).

Atlantic salmon and brown trout display a continuum of migratory strategies, ranging from downstream-upstream movements within a single river (fluvial–adfluvial potamodromy), to movements between a river and a lake (lacustrine–adfluvial potamodromy), to movements between a river system and the sea (anadromy) (Ferguson, Reed and Prodöhl, 2017; Nevoux et al., 2019). Although some non-anadromous populations exist (Hutchings et al., 2019; Berg, 1985), long-distance anadromous migration is a defining feature of most Atlantic salmon populations, facilitating rapid marine growth while the constant absence of one or more cohort from a river system provides a safeguard against extirpation in the case of sudden catastrophic events in the freshwater environment (Birnie-Gauvin, Thorstad and Aarestrup, 2019; Klemetsen et al., 2003; Jonsson and Jonsson, 2011). In contrast, brown trout are regarded as facultative, as opposed to obligate, migrants,

with many populations comprised of a mixture of individuals that display resident, potamodromous or anadromous life history strategies (Nevoux et al., 2019).

Sensitive olfactory organs allow salmonids to recognise extremely diffuse chemical signals in aquatic environments and thereby return to areas that they 'imprinted' on as juveniles when they are ready to reproduce (Dittman and Quinn, 1996; Doving, Westerberg, & Johnsen, 1985; Quinn, 1990; Tierney et al., 2008). Such reproductive homing to natal rivers regularly exceeds 95% amongst anadromous salmonids, yet 'straying' (i.e. natal dispersal) between river systems or between areas within river systems does occur (Keefer et al., 2014; Lucas et al., 2001). Straying, whether an alternative life history strategy or a product of inaccurate homing, may offer significant fitness benefits to individuals, particularly in situations where the quality or accessibility of spawning habitat in the natal river varies temporally. Straying also allows salmonids to colonise new regions or recolonise areas after extirpations (Ferguson, 2004) and provides a source of gene flow between geographically separated populations. Thus, the frequency and direction of natal dispersal between areas has numerous biological implications.

Contemporary threats to migratory salmonids

Although migratory behaviour has allowed salmonids to colonise wide geographic ranges, recolonise areas after extirpations, and take advantage of differing opportunities found in different habitats, it also exposes fish to the accumulated threats and challenges associated with each encountered habitat. As contemporary environmental changes occur at an unprecedented rate, Atlantic salmon and brown trout in many regions face uncertain futures (Jonsson and Jonsson, 2009; Kovach et

al., 2019). Indeed, Atlantic salmon are already extirpated from most river systems throughout the southern part of their historical range with a general pattern of declining populations throughout intermediate latitudes and comparatively stable populations in the far north where human population density is at its lowest (Chaput, 2012; Parrish et al., 1998). Similarly, despite their IUCN 'Least Concern' status, brown trout have disappeared from many rivers and lakes, particularly in the south of their native range, while anadromous individuals from various populations in more northerly latitudes have suffered extremely high migrant mortality in recent years (Muhlfeld et al., 2019; Poole et al., 2007; Thorstad and Finstad, 2018; Gargan, Poole and Forde, 2006).

In many cases, anthropogenic activities have been identified as the key factors contributing to the decline of Atlantic salmon and brown trout populations. Alterations to freshwater ecosystems including acidification and pollution, flow regulation, the construction of dams, fresh water extraction, arterial drainage and alien species introductions have all contributed to localised reductions in freshwater survival (Muhlfeld et al., 2019; Forseth et al., 2017). Indeed, as a result of such direct anthropogenic influences, general biodiversity in freshwater environments is now considered to be significantly more imperilled than in terrestrial or marine habitats (Strayer and Dudgeon, 2010). However, anthropogenic factors have also had severe negative influences on the marine survival rates of Atlantic salmon and brown trout in recent decades. Commercial marine fisheries have significantly increased marine mortality, whether Atlantic salmon and anadromous brown trout are specifically targeted or whether they are the unintended bycatch of other fisheries (Crozier and Kennedy, 1994; Dempson et al., 2001; Degerman, Leonardsson and Lundqvist, 2012). In addition, climate change, rising ocean temperatures and

associated changes in ocean currents are expected to alter migratory phenologies while potentially increasing mismatches between optimal migratory conditions (including prey availability) and those encountered by salmonid migrants (Edwards and Richardson, 2004; Kovach et al., 2019; Otero et al., 2014). Such mismatches have the capacity to compromise salmonid populations by reducing osmoregulatory and antipredator performance, marine growth, and, ultimately, survival.

On a more regional scale, the salmon aquaculture industry has been identified as a leading factor in the decline of numerous wild Atlantic salmon and anadromous brown trout populations (Bjorn et al., 2001; Shephard et al., 2016; Shephard and Gargan, 2017; Thorstad et al., 2015; Thorstad and Finstad, 2018). Since the establishment of modern Atlantic salmon aquaculture in the late 1960s (Knapp, Roheim and Anderson, 2007), the proliferation of salmon farms has been so extensive that, presently, ~ 98% of the total biomass of Atlantic salmon is a product of the aquaculture industry (Parrish et al., 1998). Open-cage salmon farming negatively impacts wild salmonid populations in two key ways. Firstly, through transmission of parasite or disease-induced pathological effects to wild migrants and, secondly, through the dilution or erosion of locally-adapted genetic traits in wild populations as a result of interbreeding between wild and escaped farmed salmon (Forseth et al., 2017).

A variety of bacterial and viral diseases, some of which are novel, negatively affect the marine phase of Atlantic salmon aquaculture. These include amoebic gill disease, pancreas disease, furunculosis, *Mycobacterium chelonae, Piscirickettsia salmonis,* ulcerative dermal necrosis and HSMI (Bakke and Harris, 1998; Adams and Nowak, 2004; Bruno et al., 1998; Kongtorp, Taksdal and Lyngøy, 2004; Murphy et al., 1992; Olsen et al., 1997). As high density salmon farms provide ideal conditions for the

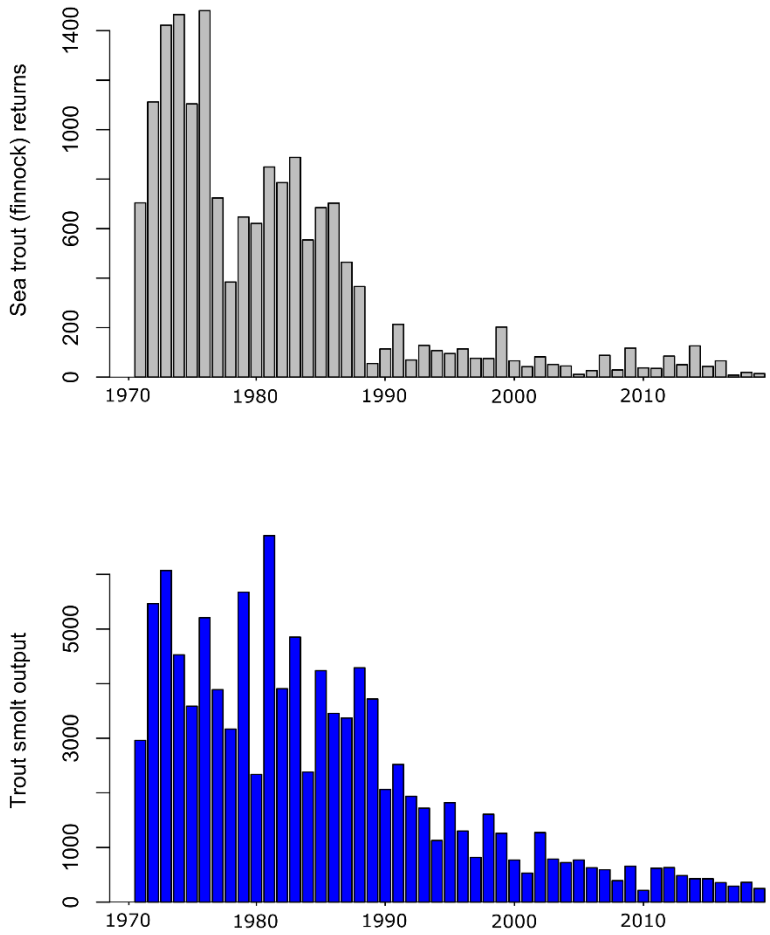
proliferation of disease and are commonly located close to the migratory routes of anadromous salmonids, infections can pass from farmed salmon to wild migrants (Forseth et al., 2017; Bakke and Harris, 1998). In a similar manner, salmon farms act as a key source of parasitic infection for many wild anadromous salmonid populations. The most notable of these parasites is the salmon louse (*Lepeophtheirus salmonis*), an ectoparasitic copepod that naturally infects wild Atlantic salmon and brown trout in the marine environment.

Migratory performance and variation in life history strategies

As with infectious diseases, high density salmon farms provide optimal conditions for sea lice to multiply, and sea lice-induced pathologies (whether resulting in reduced growth or death of the host fish) combined with control measures are estimated to cost the aquaculture industry in excess of €300,000,000 annually (Abolofia, Wilen and Asche, 2017; Costello, 2009). Historically, salmon lice on wild salmonids were observed in moderate numbers, but the proliferation of open net salmon farming has significantly increased lice production in aquaculture areas and salmon lice epizootics have been reported in Ireland, Scotland, Norway and Canada since the 1980s (Thorstad et al., 2015; Forseth et al., 2017). Studies in these countries have shown that salmon lice from aquaculture have increased marine mortality of some Atlantic salmon populations by up to 40% in recent decades, although there is wide variation between years and locations (Gargan et al., 2012; Gargan, Tully and Poole, 2003; Forseth et al., 2017; Thorstad and Finstad, 2018).

In contrast to salmon smolts which migrate rapidly through coastal areas toward open-ocean feeding grounds (e.g. Moore et al., 2008), the coastal roaming patterns of

anadromous brown trout (colloquially known as sea trout) can place them in proximity to areas of intensive aquaculture for extended periods, prolonging their exposure to lice originating in salmon farms and increasing lice-induced mortality rates (Thorstad et al., 2015; Thorstad and Finstad, 2018). For example, production of farmed salmon along the west coast of Ireland increased by roughly 400 % between 1986 and 1989 (Anon., 1984) and the first salmon farms were installed in Clew Bay in 1986 (Coughlan et al., 2006). Heavy infestations of juvenile (nauplius) *L. salmonis* on anadromous brown trout were first observed along the west coast of Ireland in 1989, the year in which the marine survival of juvenile brown trout in the region (as recorded at the tidal limit fish traps of the Burrishoole catchment, Clew Bay), which had previously ranged between 8.5% and 32.4% (mean = 21%), fell to just 1.5% (Poole et al., 1996; Whelan, 2010; Gargan et al., 2003). Tully and Whelan (1993) estimated that, by this period, ~ 95% of *L. salmonis* in the region originated in local salmon farms, and marine survival of local brown trout has remained low (mean = 6.8%) in subsequent years (Poole et al., 2007). The spawning escapement collapse of anadromous brown trout from the Burrishoole catchment was followed by a severe decline in trout smolt output from the catchment in the ensuing years (Fig. 1) despite an apparent abundance of non-anadromous trout in the catchment (Poole et al., 2007).



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Figure 1. Annual number of young sea trout (finnock) returning to the Burrishoole catchment (grey bars) and trout smolts migrating from the Burrishoole catchment to the sea (blue bars) between 1971 and 2019, as recorded at the Salmon Leap and Mill Race traps.

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These patterns provide a rare insight into the factors controlling intraspecific phenotypic diversity and suggest that, in this particular population, the propensity to go to sea is under strong genetic control and that the reduction in anadromous spawners has caused a significant evolutionary change by reducing the genetic

250 propensity for marine migration in the population. Similarly, Sandlund and Jonsson (2016) found that potamodromous migration in a Norwegian population of brown

trout ceased within a few decades of habitat alterations that reduced the growth benefits of migrating from their natal tributary to the main stem of the river. However, recent research indicates that migratory decisions in brown trout are governed by a more complex interplay between intrinsic and extrinsic factors in the sense that environmental conditions and physiology (i.e. nutritional status) may interact with locally adapted, genetically determined thresholds to shape life history strategies and migratory phenologies (Archer et al., 2019, 2020; Ferguson et al., 2019; Nevoux et al., 2019). As intraspecific variation and associated evolutionary potential provides resilience to environmental change (Schindler, 2019; Reed et al., 2011), understanding and preserving the sources of such variation within and among populations is a key conservation concern.

Active migration, whether conducted in terrestrial, aerial or aquatic environments, carries energetic costs and mortality risks. The ultimate drivers of resident or migratory life histories may be thought of as the evolutionary products of fitness trade-offs between such costs and the benefits of moving between habitats (Chapman et al., 2014). In comparison with potamodromy, anadromous migration carries the additional and significant physiological burden of maintaining osmotic homeostasis (internal osmolality and electrolyte balance) in hyperosmotic (saltwater), as well as hypoosmotic (freshwater), environments (Dawson et al., 1999). The ability of salmonids to hypo-osmoregulate (i.e. osmoregulate in salt water) effectively is critical to their survival in marine environments and can be disrupted by various factors. Crucially, the physiological condition of smolts when leaving fresh water plays a central role in determining osmoregulatory performance at sea (McCormick et al., 2009; Zydlewski, Zydlewski and Danner, 2010). Factors such as exposure to episodic acidification, industrial contaminants or pesticides in natal rivers have been

shown to reduce hypo-osmoregulatory ability and increase mortality of smolts when transferred to seawater (Finstad et al., 2007; Moore et al., 2003, 2008).

In Norway, the introduced freshwater ectoparasite *Gyrodactylus salaris* has had a devastating impact on infested Atlantic salmon populations, leading to more extirpations in that country than any other factor (Forseth et al., 2017; Johnsen and Jensen, 1986, 1991). Although *G. salaris* cannot survive in salt water, the damage that this parasite causes to salmon parr in fresh water can lead to osmoregulatory failure and mortality in the marine environment (Pettersen et al., 2013). The mechanism by which *G. salaris* causes osmoregulatory failure in smolts is functionally analogous to that of sea lice: by causing mechanical damage to the epidermis of the host, a critical organ in teleost osmoregulation (i.e. as an osmotic barrier), control of osmotic water loss is reduced and osmotic homeostasis cannot be maintained (Grimnes and Jakobsen, 1996; Pettersen et al., 2013). In addition to *G. salaris*, Atlantic salmon and brown trout act as hosts to a wide variety of freshwater ecto- and endo-parasites (Kennedy, 1974; Fitzgerald and Mulcahy, 1983). Although some of these parasites can cause significant damage to the organs involved in teleost osmoregulation (Dezfuli et al., 2002b; a, 2008; Wanstall, Robotham and Thomas, 1986; Wanstall, Thomas and Robotham, 1988), research on their potential pathological effects on salmonids in salt water is generally lacking. In Chapter 2 I have therefore investigated whether the Irish strain of the acanthocephalan endoparasite *Pomphorhynchus laevis*, which, peculiarly for this species, uses salmonids as its preferred definitive host, affects the osmoregulatory performance or stress levels of Atlantic salmon smolts in either fresh or salt water environments. As with *G. salaris* and *L. salmonis, P. laevis* causes damage to a key organ in teleost hypo-osmoregulation, the intestine.

Proximate and ultimate drivers of spatiotemporal movements

Contemporary climate change is having differing impacts on the temperature regimes of freshwater and marine environments due, in part, to differences in thermal mass (O' Reilly et al., 2015; Scanes, Scanes and Ross, 2020; Hobday and Lough, 2011; Jones, 2010). As such, freshwater cues may become increasingly unreliable predictors of marine temperatures, which, in turn, play a central role in determining prey availability for salmon at sea with important implications for marine growth and survival rates (Hvidsten et al., 2009; Kennedy and Crozier, 2010; Marschall et al., 2011; Russell et al., 2012; Thorstad et al., 2012; Zydlewski et al., 2014; Todd et al., 2011; Carr-Harris et al., 2018). Salmonid hypo-osmoregulatory efficiency is also strongly influenced by the temperature of salt water (Oppedal et al., 1999; Handeland et al., 2014, 1998), and the impact of rising marine temperatures on osmoregulatory performance is predicted to cause the loss of salmonid anadromy from southern regions (Nevoux et al., 2019; McCormick, Shrimpton and Zydlewski, 1996). Additionally, Staurnes et al. (2001) found that hypo-osmoregulatory function in Atlantic salmon smolts is significantly reduced when a temperature difference of > 4 - 6 °C exists between natal freshwater and marine environments at the time of sea entry. Furthermore, hypo-osmoregulatory efficiency and saltwater tolerance in salmonids are temporally variable, rising to a state of peak preparedness for sea entry during a period known as the physiological smolt window and then declining if fish remain in fresh water (McCormick, 2012). Thus, disruptions to the migratory phenology of smolts or the decoupling of freshwater migratory cues from marine conditions may cause a phenotype-environment mismatch and result in reduced marine performance (Barlaup et al., 2018).

In additional to broader (i.e. seasonal) phenological patterns, the fine-scale timing of migratory movements can play a key role in determining the conditions encountered during migration and in destination habitats (Schindler, 2019; Keefer et al., 2018). Several studies have shown that salmonid survival during migration can vary substantially depending on when movements through particular habitats are commenced (Jonsson, Jonsson and Jonsson, 2017; Furey et al., 2016; McLennan et al., 2018; Schwinn et al., 2017). For example, Flávio et al (2019) found that smolts moving from the River Bush in Northern Ireland into the sea during the day suffered immediate mortality rates of nearly 30 %, probably due to predation, while their nocturnally-moving counterparts suffered mortality rates of only 5 %. Such temporal variation in migratory mortality rates abounds in nature, and many species limit their movements through or between habitats to times when their exposure to threats is reduced or safe passage is facilitated (Lank et al., 2003; Lampart, 1989; Morrison, 1978; Lockard and Owings, 1974; Pechmann and Semlitsch, 1986; Bentley et al., 2014; Kotler, Brown and Hasson, 1991). To achieve this, animals use a diverse range of environmental cues to guide their movements so as to minimise mortality and optimise their migration timing (L. G. Crozier et al., 2008; Haraldstad et al., 2016; Thomas P. Quinn & Adams, 1996; Reed et al., 2006; Odd Terje Sandlund et al., 2017; Sutherland & Predavec, 1999; Williams, Barnes, & Buck, 2014, Tom P. Quinn, 2018). Whether a species uses cues associated with photoperiod, temperature, tidal movements, barometric pressure, rainfall, moon phase or any other environmental variables, many populations appear to exhibit distinct, locally-adapted responses that have historically increased fitness in their population-specific context (Mobley et al., 2019; O'Toole et al., 2015; Kawecki and Ebert, 2004). However, as modern environmental changes occur and progress, the relationship between such

cues and optimal behavioural responses are likely to be altered, leading to potential fitness loss for populations that fail to adapt rapidly (Winkler et al., 2014; McNamara et al., 2011; Reed et al., 2011).

While the environmental drivers of the migratory phenology of juvenile salmonids (i.e. smolts) have been the focus of numerous studies (see Aldvén, Degerman, et al., 2015; Aldvén, Hedger, et al., 2015; Antonsson et al., 2010; Barlaup et al., 2018; Byrne et al., 2003, 2004; Carr-Harris et al., 2018; Fraser et al., 1995; Furey et al., 2016; Haraldstad et al., 2016; Harvey et al., 2020; Honkanen et al., 2018; Hvidsten et al., 1995; Jensen et al., 2012; Jonsson and Ruud-Hansen, 1985; McCormick et al., 2002; Mclennan et al., 2018; Moore et al., 1998; Otero et al., 2014; Schwinn et al., 2019; Scheuerell et al., 2009; Winter et al., 2016), our understanding of the relationships amongst environmental factors and the fine-scale spatiotemporal movements of mature salmonids during the spawning period remains somewhat less complete. Spawning-related movements in salmonids encompass a wide variety of behaviours with diverse phenologies, directionalities, ranges, durations and associated risks (Finstad et al., 2005; Bentley et al., 2014; Quinn, McGinnity and Reed, 2016; Quinn, Unwin and Kinnison, 2000). Contrasting findings from available studies on individual populations suggest that the environmental factors used as movement cues by mature brown trout, as well as the precise behavioural responses to variation in these factors, vary significantly amongst populations (Ovidio et al., 2002; Hellawell, Leatham and Williams, 1974; Burrell et al., 2000; Bunnell and Isely, 1998; Dahl et al., 2004; Diana, Hudson and Clark, 2004; Moore et al., 2012; Slavík et al., 2012; Jonsson, 1991; Rustadbakken et al., 2004), suggesting that localised environmental conditions have driven the evolution of differing locally adapted behaviours. Thus, the identification of relationships between environmental

cues and locally adapted behavioural responses in environments that remain relatively pristine may yield valuable insights into the ultimate drivers of contemporary behaviours. Such insights may allow us to predict how specific environmental changes will affect behaviour, phenology and population performance over various time scales. Against this background, Chapter 4 describes an investigation into the associations between environmental factors and the timing of spawning-related movements of brown trout while providing conjecture on the evolutionary pressures underlying these associations.

Natal philopatry, genetic structure and local adaptation

Atlantic salmon and brown trout exhibit extensive genetic diversity amongst their populations at a wide range of spatial scales, and this genetic diversity (which encompasses locally adapted traits) is regarded as profoundly important for population persistence and productivity (Robertsen et al., 2014; Ferguson, 2003; Manhard, Joyce and Gharrett, 2017). Common garden experiments have revealed that closely neighbouring populations of Atlantic salmon can possess markedly different genetically-determined development schedules, migratory phenologies, dispersal patterns and pathogenic resistances that significantly reduce the lifetime fitness of individuals in non-native habitats relative to that of local individuals and vice versa (McGinnity et al., 2007; O'Toole et al., 2015; de Eyto et al., 2011). Indeed, by eroding locally adapted traits, interbreeding between farm escapes and native salmon leads to reduced recruitment and is regarded as a substantial threat to the persistence of wild populations (McGinnity et al., 2009; Coughlan et al., 2006; Jonsson, Jonsson and Hansen, 1991; Forseth et al., 2017). As an example of such local adaptation, the incidence of spring salmon (i.e. mature salmon that return to

natal rivers in the spring prior to the winter in which they spawn) is highest in river systems that contain safe holding habitat (Reed et al., 2017). This pattern suggests that populations have evolved to adopt this strategy most commonly in locations where low rates of freshwater adult mortality allow spring salmon to minimise cumulative (i.e. freshwater and marine) mortality risks which are traded-off against the growth benefits of additional marine feeding.

However, such examples of local adaptation in Atlantic salmon are somewhat eclipsed by the variety of genetically-based phenotypic diversity found amongst brown trout populations. Striking variation in the appearance, ecology and behaviour of brown trout led naturalists of the 19th century to describe 57 distinct species, including roughly 20 in Ireland and Britain (Ferguson, 2003). While debate continues as to whether brown trout should be regarded as a single species or a complex of species, genetic structure amongst populations is undeniably extensive and five major evolutionary groups have been described (McKeown et al., 2010; Bernatchez, 2001). For example, three genetically, morphologically and behaviourally distinct populations of brown trout from at least two genetic lineages are found in Lough Melvin, Ireland (Cawdery and Ferguson, 1988). Although no physical barriers prevent these sympatric populations from interbreeding, they have maintained their temporally stable genetic heterogeneity through differing reproductive behaviours and, in particular, by migrating to different areas for spawning (i.e. natal philopatry) (McKeown et al., 2010; Ferguson, 1989).

Such behaviourally-based reproductive isolation and genetic differentiation appears to be particularly common amongst potamodromous brown trout populations that migrate between separate natal spawning streams and shared feeding lakes (Duguid, Ferguson and Prodöhl, 2006; Swatdipong et al., 2010; Linløkken, Johansen and

Wilson, 2014; Massa-Gallucci et al., 2010; Palmé, Laikre and Ryman, 2013). However, the minimum spatial scales at which natal philopatry operates amongst spawning streams that flow into or out of lakes, and the associated patterns of gene flow and genetic structure that occur amongst such adjacent streams, remains unknown. Investigation of these behavioural and genetic patterns at a microgeographic scale (*sensu* Richardson et al., 2014) is likely to provide valuable insights into the appropriate spatial scales for salmonid management and shed further light on the threats that introgression of non-local alleles from farm escapes and stocking measures are likely to have on the fitness of locally adapted native populations. Chapter 5 represents such an investigation.

Methods for tracking the spatial behaviour of fish in freshwater environments

Rudimentary life history information such as migratory routes, movement timings or the locations of reproductive and foraging areas is essential to our understanding of animals in relation to their environment and can facilitate investigation into many of the ecological and evolutionary processes discussed thus far. Research on the movement patterns of migratory fishes has historically been hindered by the inherent difficulties involved in the observation and tracking of mobile organisms in aquatic environments. Fish trapping, in conjunction with the use of external identification tags or marks, has been used to monitor the freshwater movements of salmonids in various countries since the middle of the twentieth century (Allen, 1940; Poole et al. 1996; Byrne et al., 2003, 2004; Gard and Bottorff, 2014; Youngson et al., 1983), yet these methods generally require significant investments in infrastructure and labour,

fail to record the precise timing of movements, and can negatively affect populations by causing damage or stress to individuals or by impeding migratory movements (Beere, 1993; Music, Hawkes and Cooperman, 2010; Hansen, 1988). More recently, new technologies have been developed that allow fish to be tracked without causing impediment to their movements. However, each of these technologies carries distinct advantages and limitations. Infrared, sonar, DIDSON and resistance-based fish counters allow the passage of untagged fish to be recorded at a particular fluvial location, producing accurate detection times and an estimate of fish sizes but no way of identifying individual fish (Baumgartner et al., 2010). Coded wire microtags allow small fish to be tagged with minimal stress and financial cost, yet subsequent identification requires the recapture and sacrifice of tagged fish. Acoustic tags, radio tags and satellite tags provide the ability to track the movements of fish over large distances but their physical sizes preclude their use in small fish, their battery lives are limited and their price can be prohibitive (Cooke et al., 2013).

Miniature passive integrated transponder (PIT) tags were developed in the mid-1980s (Skalski, Smith, Iwamoto, Williams, & Hoffmann, 1998; Prentice, Flagg, & McCutcheon, 1990), and have since proven to be invaluable tools for studying fish movement in fluvial environments (Dodd, Cowx and Bolland, 2018, 2017; Barlaup et al., 2018; Letcher et al., 2018; Zydlewski et al., 2001, 2006; Lucas et al., 2000). Miniature (i.e. 12 mm x 2 mm, 0.1g) PIT tags are small enough to be implanted in salmonid parr of > 60 mm fork length (Zydlewski et al., 2006), cheap enough to be used in modestly funded studies (i.e. ~ €1.50 per tag), have no batteries (and therefore no battery life limitation), provide individual-level identification and can be detected passively by fixed stations (i.e. PIT antennae) without any need to impede fish passage. However, PIT tags have limited read ranges (usually < 1 m),

meaning that PIT antennae often need to be installed in a vertical 'pass through' orientation across rivers in order to detect tags throughout the water column (Zydlewski et al., 2006). This orientation makes traditional PIT antennae vulnerable to catastrophic damage from debris in flood-prone rivers and has thereby limited their usefulness in such systems. Thus, there is currently an evident need for PIT antenna designs that can withstand the passage of fluvial debris without suffering substantial damage (Cooke et al., 2013). In Chapter 3 I outline a novel PIT antenna design that fulfils these requirements.

The Burrishoole catchment

Habitats that remain relatively unaltered by modern anthropogenic activities present valuable opportunities to study the ultimate and proximate causes of animal behaviour as well as the interplay between behaviour, landscape features and gene flow that collectively determine spatial patterns of genetic structure and adaptation. Such ecosystems can also allow us to identify sources or regions of migratory mortality and provide crucial baselines against which to compare modern demographic patterns, yet these unspoiled areas are becoming increasingly rare (Tilman et al., 2001; Northcote, 1992; Liermann et al., 2012; Magurran, 2009). The Burrishoole catchment in north west Mayo, Ireland, is a prime example of a freshwater ecosystem that, despite experiencing moderate anthropogenic impacts (de Eyto et al., 2016), has escaped many of the severe alterations and degradations that have afflicted other Irish river systems over the last century (Riley et al., 2018; Heaney et al., 2001). In addition, Burrishoole possesses extensive infrastructure for monitoring fish movements and long time series data on salmonid behaviour and demographics. As such, the Burrishoole catchment provides an ideal setting in which

to investigate many of the ecological patterns and processes discussed previously and, for this reason, Burrishoole was chosen as the study site for all research presented in the following chapters.

Situated in a south-west facing valley within the Nephin Beg mountain range and draining into the North-east Atlantic, Burrishoole has a temperate, oceanic climate with relatively cool summers and mild winters. Mean annual rainfall in the catchment has exceeded 1600 mm in recent years (Doyle et al., 2019) and there appears to have been a trend towards higher winter temperatures over recent decades (Woolway et al., 2019). Soils throughout the catchment are composed of poorly drained gleys, peaty podsols, and blanket peats (Gardiner and Ryan, 1969), while the underlying geology is primarily comprised of quartzite and schist that, in the eastern side of the catchment, are interspersed with veins of volcanic rock, dolomite, and wacke (Whittow, 1974). As a result of these geological patterns, the western side of the catchment is strongly affected by acid runoff while the eastern side is comparatively well buffered and exhibits greater aquatic production. The river system is comprised of over 45 km of small rivers and streams that link two main freshwater lakes, Bunaveela Lough (46 ha) and Lough Feeagh (410 ha), and ultimately flow into Lough Furnace (141 ha), a brackish, partially tidal lake opening into Clew Bay (Whelan et al., 1998; Matthews et al., 1997).

Human population density in the surrounding area has been consistently low and the majority of land is currently used for low intensity sheep grazing interposed with some areas of coniferous forestry. Commercial afforestation in the catchment first commenced in the 1950s and a period of intensive sheep overgrazing in the late 1980s and 1990s, associated with European Union headage payments (Bonn et al., 2009), caused erosion within the catchment to increase and led to elevated levels of

nutrients (mainly phosphate), sediment and organic matter in the river system (Dalton et al., 2014). However, despite this increase in sedimentation, de Eyto et al (2016) found that these changes in land use throughout the catchment have had no significant impact on the freshwater survival of Atlantic salmon or brown trout.

While the geology, soil types, climate and physical complexity of the Burrishoole catchment make it comparable to numerous coastal humic river systems in the west of Ireland, it has the distinction of being one of only 13 international index sites collecting long-term data on diadromous salmonids and the European eel (*Anguilla anguilla* L.) in the North-east Atlantic region (Prévost et al., 2003). Full daily trapping of fish moving upstream or downstream has been conducted at the tidal limit of the catchment since 1970, providing one of the longest and most comprehensive such data sets in existence (Poole, Reynolds and Moriarty, 1990; Poole et al., 1996; Gargan, Poole and Forde, 2006; Byrne et al., 2004, 2003b; Sandlund et al., 2017). Extensive complementary research into local hydrology, carbon cycling, parasite communities, zooplankton and macroinvertebrate abundance patterns, climate variation and lake-bed geochemistry (Andersen et al., 2020; Byrne, Holland, et al., 2003; Dalton et al., 2018; Doyle et al., 2019; de Eyto et al., 2019; Kelly et al., 2018; Molloy et al., 1993; Woolway et al., 2019) make the Burrishoole catchment one of the most intensively studied freshwater ecosystems in Europe. Due to the attributes described here, the Burrishoole catchment provides unparalleled opportunities for conducting novel salmonid research.

Objectives and overview of thesis

The overarching objective of this thesis was to investigate the interplay between environmental heterogeneity in its broadest sense (i.e. including spatial and temporal variation of biotic and abiotic factors) and locally-adapted migratory behaviours, dispersal patterns, genetic structure and physiological performance using wild Atlantic salmon and brown trout as case study animals.

In Chapter 2 I sought to determine whether the Irish freshwater strain of the acanthocephalan ectoparasite *Pomphorhynchus laevis* affected osmoregulatory performance or stress levels in infected Atlantic salmon smolts in fresh or salt water environments. A habitat-specific pathology could influence migratory performance and thereby constitute a selective pressure for a particular life history strategy. I characterised infection prevalence and intensity patterns amongst wild Atlantic salmon smolts captured from the Burrishoole catchment over a three-year period and investigated whether infection was associated with variation in osmoregulatory performance (as measured by plasma chloride) or stress (as measured by blood glucose and plasma cortisol) in fresh or salt water. Additionally, I investigated whether the local strain of *P. laevis* could survive in salmonid hosts in a salt water environment for periods of 24 to 72 hours.

Chapter 3 takes the form of a technical description focused on the design and implementation of a novel double-breakaway pass-through PIT antenna system I developed for use in flood-prone rivers. The aim of this chapter was to provide a flexible design framework for fluvial telemetry research that would increase data continuity while decreasing long-term maintenance requirements.

In Chapter 4 I explored associations between environmental variables and the seasonal, daily and diel movement patterns of mature brown trout between a feeding lake and two spawning streams (one inflow and one outflow) with the aim of identifying the proximate drivers of temporal spawning movements through transitional areas between habitats. I discuss observed behavioural patterns in the context of their potential ultimate causes.

In Chapter 5 I aimed to investigate whether microgeographic genetic structure (*sensu* Richardson et al., 2014) may arise and persist amongst potamodromous brown trout that feed in a shared lake, and to identify the interactions between behaviour and landscape that underlie such structure. To this end, I used a combination of PIT-derived data and genetic analyses to investigate the interplay between gene flow, genetic differentiation and the spawning movements of mature brown trout between a feeding lake and two spawning streams. Findings are discussed in terms of their implications for the spatial scale of local adaptation and management units.

Each of these chapters (2-5) contains a specific introduction, review of the relevant literature, methodology, results and discussion. Chapter 6 provides a synthesis of the overall findings and discusses avenues for prospective research.

I have included four Appendices which contain additional research I have been involved in during my studies and that is of relevance to the overall research objectives of the project. Appendix A presents a number of findings from a complementary branch of investigation on Atlantic salmon smolts that I pursued during my studies and that I am preparing for publication in the near future. These findings are briefly discussed in Chapter 6 and are used to illustrate the universality or specificity of results described the preceding chapters. Appendix B takes the form

of an executive summary of the WGTRUTTA Draft Final Report (2020). WGTRUTTA is an ICES working group established in 2017 with the aim of developing assessment models and establishing biological reference points for anadromous brown trout populations. I have been a participating member of the group since its establishment. Appendix C constitutes a published review of existing literature on the influence of environmental heterogeneity on life history strategies in brown trout with a particular focus on the factors associated with anadromous and freshwater resident life histories. Appendix D provides a published characterisation of the diet of juvenile brown trout and Atlantic salmon in the Burrishoole catchment as revealed by stomach content analyses and stable isotope analyses.

Articles and contributions

(My contributions are shown in italicized text)

Finlay, R., Poole, R., Rogan, G., Cotter, D., Reed, T.E. Hyper- and hypo-osmoregulatory performance of Atlantic salmon (*Salmo salar*) smolts infected with *Pomphorhynchus laevis* (Acanthcephala) (In preparation for submission) (*Collected, processed and analysed the data and wrote the first draft of the paper*.)

Finlay, R., Poole, R., French, A.F., Phillips, K.P., Kaufmann, J., Doogan, A., Cotter, D., McGinnity, P., Reed, T.E. 2020. Spawning-Related Movements in a Salmonid Appear Timed to Reduce Exposure to Visually-Oriented Predators. Animal Behaviour (In review). (*Collected, processed and analysed the data and wrote the first draft of the paper*.)

Finlay, R., Poole, R., Coughlan, J., Phillips, K.P., Prodöhl, P., Cotter, D., McGinnity, P., Reed, T.E. 2020. Telemetry and Genetics Reveal Asymmetric Dispersal of a Lake-Feeding Salmonid between Inflow and Outflow Spawning Streams at a Microgeographic Scale. Ecology and Evolution 10, (4): 1762–83. https://doi.org/10.1002/ece3.5937 (*Collected, processed and analysed the data and wrote the first draft of the paper*.)

Finlay, R., Reed, T., Poole, R. 2020. Development of a Double-Breakaway Pass-through PIT-Tag Antenna System for Flood-Prone Rivers. North American Journal

of Fisheries Management. https://doi.org/10.1002/nafm.10454 (In press) (*Developed the antenna system and wrote the first draft of the paper*.)

Nevoux, M., Finstad, B., Davidsen, J.G., **Finlay, R.,** Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O., Jonsson, B. 2019. Environmental Influences on Life History Strategies in Partially Anadromous Brown Trout (Salmo Trutta, Salmonidae). Fish and Fisheries 20(6):1051–82. https://doi.org/10.1111/faf.12396 (*Contributed to the initial development of the paper, provided 15 - 20% of the text in the first draft and participated in the final writing/discussion phase.*)

de Eyto, E., Doyle, B., King, N., Kilbane, T., **Finlay, R**., Graham, C., Poole, R., Ryder, E., Dillane, M., Jennings, E. 2020. Characterisation of Salmonid Food Webs in the Rivers and Lakes of an Irish Peatland Ecosystem. Biology and Environment: Proceedings of the Royal Irish Academy 120(1):1–17. https://doi.org/10.3318/bioe.2020.01 (*Provided data, SIA samples and participated in the final writing/discussion phase.*)

References

Abolofia, J., Wilen, J.E. and Asche, F., 2017. The cost of lice: Quantifying the impacts of parasitic sea lice on farmed salmon. *Marine Resource Economics*, 32(3), pp.329–349.

Abrahms, B., Hazen, E.L., Aikens, E.O., Savoca, M.S., Goldbogen, J.A., Bograd, S.J., Jacox, M.G., Irvine, L.M., Palacios, D.M. and Mate, B.R., 2019. Memory and resource tracking drive blue whale migrations. *Proceedings of the National Academy of Sciences of the United States of America*, 116(12), pp.5582–5587.

Adams, M.B. and Nowak, B.F., 2004. Sequential pathology after initial freshwater bath treatment for amoebic gill disease in cultured Atlantic salmon, Salmo salar L. *Journal of Fish Diseases*, 27(3), pp.163–173.

Aldvén, D., Degerman, E. and Höjesjö, J., 2015. Environmental cues and downstream migration of anadromous brown trout (Salmo trutta) and Atlantic salmon (Salmo salar) smolts. *Boreal Environment Research*, 20, pp.35–44.

Aldvén, D., Hedger, R., Økland, F., Rivinoja, P. and Höjesjö, J., 2015. Migration speed, routes, and mortality rates of anadromous brown trout Salmo trutta during outward migration through a complex coastal habitat. *Marine Ecology Progress Series*, 541, pp.151–163.

Allen, K.R., 1941. Studies on the Biology of the Early Stages of the Salmon (Salmo salar). *The Journal of Animal Ecology*, 10(3), pp.273–295.

Andersen, M.R., Eyto, E. de, Dillane, M., Poole, R. and Jennings, E., 2020. 13 Years of Storms : An Analysis of the Effects of Storms on Lake Physics on the Atlantic

Fringe of Europe. *Water*, 12, pp.1–21.

Anon., 1984. *Report of the Sea Trout Task Force*. Dublin.

Antonsson, T., Heidarsson, T. and Snorrason, S.S., 2010. Smolt Emigration and Survival to Adulthood in Two Icelandic Stocks of Atlantic Salmon. *Transactions of the American Fisheries Society*, 139(January), pp.1688–1698.

Archer, L.C., Hutton, S.A., Harman, L., McCormick, S.D., O'Grady, M.N., Kerry, J.P., Poole, W.R., Gargan, P., McGinnity, P. and Reed, T.E., 2020. Food and temperature stressors have opposing effects in determining flexible migration decisions in brown trout (Salmo trutta). *Global Change Biology*, 26(5), pp.2878–2896.

Archer, L.C., Hutton, S.A., Harman, L., O'Grady, M.N., Kerry, J.P., Poole, W.R., Gargan, P., McGinnity, P. and Reed, T.E., 2019. The interplay between extrinsic and intrinsic factors in determining migration decisions in brown trout (Salmo trutta): An experimental study. *Frontiers in Ecology and Evolution*, 7, pp.1–18.

Arostegui, M.C. and Quinn, T.P., 2019. Reliance on lakes by salmon, trout and charr (Oncorhynchus , Salmo and Salvelinus): An evaluation of spawning habitats, rearing strategies and trophic polymorphisms. *Fish and Fisheries*, 20(4), pp.775–794.

Bakke, T.A. and Harris, P.D., 1998. Diseases and parasites in wild Atlantic salmon (Salmo salar) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(1), pp.247–266.

Barlaup, B.T., Rund, H., Normann, E.S., Stranzl, S., Mahlum, S. and Vollset, K.W., 2018. Out of sync: monitoring the time of sea entry of wild and hatchery salmon

Salmo salar smolt using floating passive-integrated transponder antennae. *Journal of Fish Biology*, pp.1–23.

Baumgartner, L., Bettanin, M., McPherson, J., Jones, M., Zampatti, B. and Beyer, K., 2010. *Assessment of an infrared fish counter (Vaki Riverwatcher) to quantify fish migrations in the Murray-Darling Basin*. *Australian Journal of Zoology*. Cronulla.

Beere, M.C., 1993. *An Evaluation of the use of a Rotary Screw Fish Trap for Assessing Steelhead Smolt Emigrations in the Little Bulkley River, 1993*. Smithers, B.C.

Bentley, K.T., Schindler, D.E., Cline, T.J., Armstrong, J.B., Macias, D., Ciepiela, L.R. and Hilborn, R., 2014. Predator avoidance during reproduction: Diel movements by spawning sockeye salmon between stream and lake habitats. *Journal of Animal Ecology*, 83(6), pp.1478–1489.

Berg, O.K., 1985. The formation of non-anadromous populations of Atlantic salmon, Salmon salar L., in Europe. *Journal of Fish Biology*, 27(6), pp.805–815.

Bernatchez, L., 2001. The evolutionary history of brown trout (Salmo trutta L.) inferred from phylogeographic, nested clade, and mismatch analyses of mitochondrial DNA variation. *Evolution*, 55(2), pp.351–379.

Birnie-Gauvin, K., Thorstad, E.B. and Aarestrup, K., 2019. Overlooked aspects of the Salmo salar and Salmo trutta lifecycles. *Reviews in Fish Biology and Fisheries*, 29, pp.749–766.

Bjorn, P.A., Finstad, B. and Kristoffersen, R., 2001. Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. *Aquaculture Research*, 32, pp.947–962.

Bonn, A., Allott, T., Hubacek, K. and Stewart, J., 2009. *Drivers of environmental change in uplands: concepts, threats and opportunities*. Oxon: Routledge.

Bruno, D.W., Griffiths, J., Mitchell, C.G., Wood, B.P., Fletcher, Z.J., Drobniewski, F.A. and Hastings, T.S., 1998. Pathology attributed to Mycobacterium chelonae infection among farmed and laboratory-infected Atlantic salmon Salmo salar. *Diseases of Aquatic Organisms*, 33(2), pp.101–109.

Buffington, J.M., Montgomery, D.R. and Greenberg, H.M., 2004. Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness in mountain catchments. *Canadian Journal of Fisheries and Aquatic Sciences*, 61(11), pp.2085–2096.

Bunnell, D.B. and Isely, J., 1998. Diel Movement of Brown Trout in a Southern Appalachian River. *Transactions of the American Fisheries Society*, 127, pp.630–636.

Burrell, K.H., Isely, J., Bunnell, D.B., Van Lear, D.H. and Dolloff, C.A., 2000. Seasonal Movement of Brown Trout in a Southern Appalachian River. *Transactions of the American Fisheries Society*, 129, pp.1373–1379.

Byrne, C.J., Holland, C. V, Kennedy, C.R. and Poole, W.R., 2003a. Interspecific interactions between Acanthocephala in the intestine of brown trout: are they more frequent in Ireland? *Parasitology*, 127, pp.399–409.

Byrne, C.J., Poole, R., Dillane, M., Rogan, G. and Whelan, K.F., 2004. Temporal and environmental influences on the variation in sea trout (Salmo trutta L.) smolt migration in the Burrishoole system in the west of Ireland from 1971 to 2000. *Fisheries Research*, 66(1), pp.85–94.

Byrne, C.J., Poole, R., Rogan, G., Dillane, M. and Whelan, K.F., 2003b. Temporal and environmental influences on the variation in Atlantic salmon smolt migration in the Burrishoole system 1970-2000. *Journal of Fish Biology*, 63(6), pp.1552–1564.

Carlsson, J., Olsén, K.H., Nilsson, J., Øverli, Ø. and Stabell, O.B., 1999. Microsatellites reveal fine-scale genetic structure in stream-living brown trout. *Journal of Fish Biology*, 55(6), pp.1290–1303.

Carr-Harris, C.N., Moore, J.W., Gottesfeld, A.S., Gordon, J.A., Shepert, W.M., Henry, J.D.J., Russell, H.J., Helin, W.N.B., Doolan, D.J. and Beacham, T.D., 2018. Phenological Diversity of Salmon Smolt Migration Timing within a Large Watershed. *Transactions of the American Fisheries Society*, 147(5), pp.775–790.

Cawdery, S.A.H. and Ferguson, A., 1988. Origins and differentiation of three sympatric species of trout (Salmo Trutta L.) in Lough Melvin. *Polskie Archiwum Hydrobiologii*, 35(3–4), pp.267–277.

Chapman, B.B., Hulthén, K., Wellenreuther, M., Hansson, L., Nilsson, J.-åke and Brönmark, C., 2014. Patterns of animal migration. In: L.-A. Hansson and S. Åkesson, eds. *Animal Movement Accross Scales*. Oxford Scholarship Online.pp.10–35.

Chaput, G., 2012. Overview of the status of Atlantic salmon (Salmo salar) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69(9), pp.1538–1548.

Cochran, W.W., Mouritsen, H. and Wikelski, M., 2004. Migrating Songbirds Recalibrate Their Magnetic Compass Daily from Twilight Cues. *Science*, 304, pp.405–408.

Cooke, S.J., Midwood, J.D., Thiem, J.D., Klimley, P., Lucas, M.C., Thorstad, E.B., Eiler, J., Holbrook, C. and Ebner, B.C., 2013. Tracking animals in freshwater with electronic tags: past, present and future. *Animal Biotelemetry*, 1(5), pp.1–19.

Costello, M.J., 2009. The global economic cost of sea lice to the salmonid farming industry. *Journal of Fish Diseases*, 32(1), pp.115–118.

Coughlan, J., McGinnity, P., O'Farrell, B., Dillane, E., Diserud, O., de Eyto, E., Farrell, K., Whelan, K., Stet, R.J.M. and Cross, T.F., 2006. Temporal variation in an immune response gene (MHC I) in anadromous Salmo trutta in an Irish river before and during aquaculture activities. *ICES Journal of Marine Science*, 63(7), pp.1248–1255.

Cresci, A., Durif, C.M., Paris, C.B., Shema, S.D., Skiftesvik, A.B. and Browman, H.I., 2019. Glass eels (Anguilla anguilla) imprint the magnetic direction of tidal currents from their juvenile estuaries. *Communications Biology*, 2(1), pp.1–8.

Crozier, L.G., Hendry, A.P., Lawson, P.W., Quinn, T.P., Mantua, N.J., Battin, J., Shaw, R.G. and Huey, R.B., 2008. Potential responses to climate change in organisms with complex life histories : evolution and plasticity in Pacific salmon. *Evolutionary Applications*, 1(2), pp.252–270.

Crozier, W.W. and Kennedy, G.J.A., 1994. Marine exploitation of Atlantic salmon (Salmo salar L.) from the River Bush, Northern Ireland. *Fisheries Research*, 19(1–2), pp.141–155.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26, pp.249–293.

Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E. and Löf, A., 2004. The timing of spawning migration: implications of environmental variation, life history, and sex. *Canadian Journal of Zoology*, 82, pp.1864–1870.

Dalton, C., O'Dwyer, B., Taylor, D., de Eyto, E., Jennings, E., Chen, G., Poole, R., Dillane, M. and McGinnity, P., 2014. Anthropocene environmental change in an internationally important oligotrophic catchment on the Atlantic seaboard of western Europe. *Anthropocene*, 5, pp.9–21.

Dalton, C., Sparber, K. and de Eyto, E., 2018. Assessing sedimentation in a temperate dystrophic lake in the NE Atlantic seaboard region. *Journal of Paleolimnology*, 60, pp.117–131.

Davis, L.S., Boersma, P.D. and Court, G.S., 1996. Satellite telemetry of the winter migration of Adelie penguins (Pygoscelis adeliae). *Polar Biology*, 16(3), pp.221–225.

Dawson, L.H.J., Pike, A.W., Houlihan, D.F. and McVicar, A.H., 1999. Changes in physiological parameters and feeding behaviour of Atlantic salmon Salmo salar infected with sea lice Lepeophtheirus salmonis. *Diseases of Aquatic Organisms*, 35, pp.89–99.

Degerman, E., Leonardsson, K. and Lundqvist, H., 2012. Coastal migrations, temporary use of neighbouring rivers, and growth of sea trout (Salmo trutta) from nine northern Baltic Sea rivers. *ICES Journal of Marine Science*, 69(6), pp.971–980.

Dempson, J.B., Schwarz, C.J., Reddin, D.G., O'Connell, M.F., Mullins, C.C. and Bourgeois, C.E., 2001. Estimation of marine exploitation rates on atlantic salmon (Salmo salar L.) stocks in Newfoundland, Canada. *ICES Journal of Marine Science*, 58(1), pp.331–341.

Dezfuli, B.S., Giari, L., Simoni, E., Bosi, G. and Manera, M., 2002a. Histopathology, immunohistochemistry and ultrastructure of the intestine of Leuciscus cephalus (L.) naturally infected with Pomphorhynchus laevis (Acanthocephala). *Journal of Fish Diseases*, 25, pp.7–14.

Dezfuli, B.S., Lui, A., Boldrini, P., Pironi, F. and Giari, L., 2008. The inflammatory response of fish to helminth parasites. *Parasite*, 15(3), pp.426–433.

Dezfuli, B.S., Pironi, F., Giari, L., Domeneghini, C. and Bosi, G., 2002b. Effect of Pomphorhynchus laevis (Acanthocephala) on putative neuromodulators in the intestine of naturally infected Salmo trutta. *Diseases of Aquatic Organisms*, 51, pp.27–35.

Diana, J.S., Hudson, J.P. and Clark, R.D., 2004. Movement Patterns of Large Brown Trout in the Mainstream Au Sable River , Michigan. *Transactions of the American Fisheries Society*, 133, pp.34–44.

Dittman, A.H. and Quinn, T.P., 1996. Homing in Pacific salmon: mechanisms and ecological basis. *The Journal of experimental biology*, 199(1), pp.83–91.

Dodd, J.R., Cowx, I.G. and Bolland, J.D., 2017. Efficiency of a nature-like bypass channel for restoring longitudinal connectivity for a river-resident population of brown trout. *Journal of Environmental Management*, 204, pp.318–326.

Dodd, J.R., Cowx, I.G. and Bolland, J.D., 2018. Win, win, win: Low cost baffle fish pass provides improved passage efficiency, reduced passage time and broadened passage flows over a low-head weir. *Ecological Engineering*, 120, pp.68–75.

Doving, K.B., Westerberg, H. and Johnsen, P.B., 1985. Role of ofaction in the behavioral and neuronal responses of Atlantic salmon, salmo salar, to hydrographic

stratification. *Canadian Journal of Fisheries and Aquatic Sciences*, 42, pp.1658–1667.

Doyle, B.C., Eyto, E. de, Dillane, M., Poole, R., Mccarthy, V. and Jennings, E., 2019. Synchrony in catchment stream colour levels is driven by both local and regional climate. *Biogeosciences*, 16(5), pp.1053–1071.

Duguid, R.A., Ferguson, A. and Prodöhl, P., 2006. Reproductive isolation and genetic differentiation of ferox trout from sympatric brown trout in Loch Awe and Loch Laggan, Scotland. *Journal of Fish Biology*, 69(Supplement A), pp.89–114.

Edwards, M. and Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430(9), pp.881–884.

de Eyto, E., Dalton, C., Dillane, M., Jennings, E., McGinnity, P., O'Dwyer, B., Poole, R., Rogan, G. and Taylor, D., 2016. The response of North Atlantic diadromous fish to multiple stressors, including land use change: a multidecadal study. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(12), pp.1759–1769.

de Eyto, E., Kelly, S., Ryder, E., Dillane, M., Archer, L., O'Cathain, D., Daly, S., Lyons, K., Obrador, B., Brentrup, J., Naumoski, A., Poole, R., Lucy, F.E. and Jennings, E., 2019. High frequency monitoring reveals fine scale spatial and temporal dynamics of the deep chlorophyll maximum of a stratified coastal lagoon. *Estuarine, Coastal and Shelf Science*, 218, pp.278–291.

de Eyto, E., McGinnity, P., Huisman, J., Coughlan, J., Consuegra, S., Farrell, K., O'Toole, C., Tufto, J., Megens, H., Jordan, W., Cross, T. and Stet, R.J.M., 2011. Varying disease-mediated selection at different life-history stages of Atlantic salmon in fresh water. *Evolutionary Applications*, 4, pp.749–762.

Fedorka, K.M., Winterhalter, W.E., Shaw, K.L., Brogan, W.R. and Mousseau, T.A., 2012. The role of gene flow asymmetry along an environmental gradient in constraining local adaptation and range expansion. *Journal of Evolutionary Biology*, 25(8), pp.1676–1685.

Ferguson, A., 1989. Genetic differences among brown trout, Salmo trutta, stocks and their importance for the conservation and management of the species. *Freshwater Biology*, 21(1), pp.35–46.

Ferguson, A., 2003. Brown trout genetic diversity : origins, importance and the impacts of supplemental stocking. In: *Proceedings of the Institute of Fisheries Management 34th Annual Study Course*. pp.26–43.

Ferguson, A., 2004. The Importance of Identifying Conservation Units : Brown Trout and Pollan in Ireland. *Biology & Environment Proceedings of the Royal Irish Academy*, 104(3), pp.33–41.

Ferguson, A., Reed, T. and Prodöhl, P., 2017. Anadromy in brown trout: A review of the relative role of genes and environmental factors and the implications for management and conservation. In: *Sea Trout: Science and Management - Proceedings of the 2nd International Sea Trout Symposium*. pp.1–40.

Ferguson, A., Reed, T.E., Cross, T.F., McGinnity, P. and Prodöhl, P.A., 2019. Anadromy, potamodromy and residency in brown trout Salmo trutta : the role of genes and the environment. *Journal of Fish Biology*, 95(3), pp.692–718.

Finstad, A.G., Økland, F., Thorstad, E.B. and Heggberget, T.G., 2005. Comparing upriver spawning migration of Atlantic salmon Salmo salar and sea trout Salmo trutta. *Journal of Fish Biology*, 67(4), pp.919–930.

Finstad, B., Kroglund, F., Strand, R., Stefansson, S.O., Bjørn, P.A., Rosseland, B.O., Nilsen, T.O. and Salbu, B., 2007. Salmon lice or suboptimal water quality — Reasons for reduced postsmolt survival? *Aquaculture*, 273, pp.374–383.

Fitzgerald, R.D. and Mulcahy, M.F., 1983. Parasites of salmon Salmo salar L. and trout Salmo trutta L. in the River Shournagh. In: C. Moriarty, ed. *Irish Fisheries Investigations: Advances in Fish Biology in Ireland*. Dublin: The National Committee for Biology of the Royal Irish Academy.pp.24–31.

Flávio, H., Kennedy, R., Ensing, D., Jepsen, N. and Aarestrup, K., 2019. Marine mortality in the river ? Atlantic salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment. *Fisheries Management and Ecology*, 27(1), pp.1-92–101.

Forrest, J. and Miller-Rushing, A.J., 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), pp.3101–3112.

Forseth, T., Barlaup, B.T., Finstad, B., Fiske, P., Gjøsæter, H., Hindar, A., Mo, T.A., Rikardsen, A.H. and Thorstad, E.B., 2017. The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science*, 74(6), pp.1496–1513.

Fraser, N.H.C., Heggenes, J., Metcalfe, N. and Thorpe, J.E., 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. *Canadian Journal of Zoology*, 73, pp.446–451.

Furey, N.B., Hinch, S.G., Bass, A.L., Middleton, C.T., Minke-Martin, V. and Lotto, A.G., 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. *Journal of Animal Ecology*, 85, pp.948–959.

Gard, R. and Bottorff, R.L., 2014. *A History of Sockeye Salmon Research, Karluk River System, Alaska, 1880–2010. U.S. Dept. of Commer. NOAA Technical Memorandum NMFS-F/SPO-125*. National Oceanic and Atmospheric Administration- National Marine Fisheries Service.

Gardiner, J. and Ryan, P., 1969. A New Generalised Soil Map of Ireland and Its Land-Use. *Irish Journal of Agricultural Research*, 8(1), pp.95–109.

Gargan, P., Poole, R. and Forde, G., 2006. A review of the status of Irish Sea Trout Stocks. In: G.S. Harris and N.J. Milner, eds. *Sea Trout: Biology, Conservation and Management*. Cardiff, Wales: Blackwell Publishing Ltd.pp.25–44.

Gargan, P.G., Forde, G., Hazon, N., Russell, D.J.F. and Todd, C.D., 2012. Evidence for sea lice-induced marine mortality of atlantic salmon (Salmo salar) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(2), pp.343–353.

Gargan, P.G., Tully, O. and Poole, W.., 2003. Relationship between sea lice infestation, sea lice production and se trout survival in Ireland, 1992-2001. In: D. Mills, ed. *Salmon on the Edge*. Oxford, UK: Blackwell Publishing Ltd.pp.119–135.

Gauthey, Z., Lang, M., Elosegi, A., Tentelier, C., Rives, J. and Labonne, J., 2015. Brown trout spawning habitat selection and its effects on egg survival. *Ecology of Freshwater Fish*, 26, pp.133–140.

Grimnes, A. and Jakobsen, P.J., 1996. The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. *Journal of Fish Biology*, 49, pp.1179–1194.

Gwinner, E., 1989. Photoperiod as a modifying and limiting factor in the expression

of avian circannual rhythms. *Journal of Biological Rhythms*, 4(2), pp.237–250.

Haak, A.L. and Williams, J.E., 2013. Using native trout restoration to jumpstart freshwater conservation planning in the Interior West. *Journal of Conservation Planning*, 9, pp.38–52.

Handeland, S.O., Berge, Å., Björnsson, B.T. and Stefansson, S.O., 1998. Effects of temperature and salinity on osmoregulation and growth of Atlantic salmon (Salmo salar L.) smolts in seawater. *Aquaculture*, 168(1–4), pp.289–302.

Handeland, S.O., Imsland, A.K., Nilsen, T.O., Ebbesson, L.O.E., Hosfeld, C.D., Pedrosa, C., Toften, H. and Stefansson, S.O., 2014. Osmoregulation in Atlantic salmon Salmo salar smolts transferred to seawater at different temperatures. *Journal of Fish Biology*, 85(4), pp.1163–1176.

Hansen, L.P., 1988. Effects of Carlin tagging and fin clipping on survival of Atlantic salmon (Salmo salar L.) released as smolts. *Aquaculture*, 70(4), pp.391–394.

Hansson, L.-A. and Åkesson, S., 2014. *Animal Movement Accross Scales*. Oxford: Oxford University Press.

Haraldstad, T., Kroglund, F., Kristensen, T., Jonsson, B. and Haugen, T.O., 2016. Diel migration pattern of Atlantic salmon (Salmo salar) and sea trout (Salmo trutta) smolts: an assessment of environmental cues. *Ecology of Freshwater Fish*, 26(4), pp.541–551.

Harvey, A.C., Glover, K.A., Wennevik, V. and Skaala, Ø., 2020. Atlantic salmon and sea trout display synchronised smolt migration relative to linked environmental cues. *Nature- Scientific Reports*, 10, pp.1–13.

Heaney, S.I., Foy, R.H., Kennedy, G.J.A., Crozier, W.W. and O'Connor, W.C.K.,

2001. Impacts of agriculture on aquatic systems: Lessons learnt and new unknowns in Northern Ireland. *Marine and Freshwater Research*, 52(1), pp.151–163.

Hellawell, J.M., Leatham, H. and Williams, G.I., 1974. The upstream migratory behaviour of salmonids in the River Frome, Dorset. *Journal of Fish Biology*, 6, pp.729–744.

Hobday, A.J. and Lough, J.M., 2011. Projected climate change in Australian marine and freshwater environments. *Marine and Freshwater Research*, 62, pp.1000–1014.

Honkanen, H.M., Rodger, J.R., Stephen, A., Adams, K., Freeman, J. and Adams, C.E., 2018. Counterintuitive migration patterns by Atlantic salmon Salmo salar smolts in a large lake. *Journal of Fish Biology*, 93(1), pp.159–162.

Hutchings, J.A., Ardren, W.R., Barlaup, B.T., Bergman, E., Clarke, K.D., Greenberg, L.A., Lake, C., Piironen, J., Sirois, P., Sundt-Hansen, L.E. and Fraser, D.J., 2019. Life-History Variability and Conservation Status of Landlocked Atlantic Salmon: An Overview. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(10), pp.1697–1708.

Hvidsten, N.A., Jensen, A.J., Rikardsen, A.H., Finstad, B., Aure, J., Stefansson, S., Fiske, P. and Johnsen, B.O., 2009. Influence of sea temperature and initial marine feeding on survival of Atlantic salmon salmo salar post-smolts from the rivers Orkla and Hals, Norway. *Journal of Fish Biology*, 74(7), pp.1532–1548.

Hvidsten, N.A., Jensen, A.J., Vivas, H., Bakke, O. and Heggberget, T.G., 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. *Nordic Journal of Freshwater Research*, 70(October 2014), pp.38–48.

Jensen, A.J., Finstad, B., Fiske, P., Hvidsten, N.A., Rikardsen, A.H. and Saksgård, L., 2012. Timing of smolt migration in sympatric populations of Atlantic salmon (Salmo salar), brown trout (Salmo trutta), and Arctic char (Salvelinus alpinus). *Canadian Journal of Fisheries and Aquatic Sciences*, 69, pp.711–723.

Johnsen, B.O. and Jensen, A.J., 1986. Infestations of Atlantic salmon, Salmo salar, by Gyrodactylus salaris in Norwegian rivers. *Journal of Fish Biology*, 29(2), pp.233–241.

Johnsen, B.O. and Jensen, A.J., 1991. The Gyrodactylus Story in Norway. *Aquaculture*, 98(1–3), pp.289–302.

Jones, J.A.A., 2010. *Water Sustainability: A Global Perspective*. London: Hodder Education.

Jonsson, B., Jonsson, M. and Jonsson, N., 2017. Influences of migration phenology on survival are size-dependent in juvenile Atlantic salmon (Salmo salar). *Canadian Journal of Zoology*, 95(8), pp.581–587.

Jonsson, B. and Jonsson, N., 2006. Life History of the Anadromous Trout Salmo trutta. In: *Sea Trout: Biology, Conservation and Management*. Oxford: Blackwell Publishing Ltd.pp.196–223.

Jonsson, B. and Jonsson, N., 2009. A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. *Journal of Fish Biology*, 75, pp.2381–2447.

Jonsson, B. and Jonsson, N., 2011. *Ecology of Atlantic salmon and brown trout: Habitat as a template for life histories*. Dordrecht: Springer Netherlands.

Jonsson, B., Jonsson, N. and Hansen, L.P., 1991. Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture*, 98(1–3), pp.69–78.

Jonsson, B. and Ruud-Hansen, J., 1985. Water Temperature as the Primary Influence on Timing of Seaward Migrations of Atlantic Salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, 42, pp.593–595.

Jonsson, N., 1991. Influence of water flow, temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research*, 66, pp.20–35.

Jonsson, N., Jonsson, B. and Hansen, L.P., 1998. The relative role of density-dependent and density-independent survival in the life cycle of atlantic salmon Salmo salar. *Journal of Animal Ecology*, 67(5), pp.751–762.

Kawecki, T.J. and Ebert, D., 2004. Conceptual issues in local adaptation. *Ecology Letters*, 7, pp.1225–1241.

Kawecki, T.J. and Holt, R.D., 2002. Evolutionary Consequences of Asymmetric Dispersal Rates. *The American Naturalist*, 160(3), pp.333–347.

Keefer, M.L., Clabough, T.S., Jepson, M.A., Johnson, E.L., Peery, C.A. and Caudill, C.C., 2018. Thermal exposure of adult Chinook salmon and steelhead: Diverse behavioral strategies in a large and warming river system. *PLoS ONE*, 13(9), pp.1–29.

Kelly, S., de Eyto, E., Dillane, M., Poole, R., Brett, G. and White, M., 2018. Hydrographic maintenance of deep anoxia in a tidally influenced saline lagoon. *Marine and Freshwater Research*, 69(3), pp.432–445.

Kennedy, C.R., 1974. A checklist of British and Irish freshwater fish parasites with

notes on their distribution. *Jourtial of Fish Biology*, 6, pp.613–644.

Kennedy, R.J. and Crozier, W.W., 2010. Evidence of changing migratory patterns of wild Atlantic salmon Salmo salar smolts in the River Bush, Northern Ireland, and possible associations with climate change. *Journal of Fish Biology*, 76(7), pp.1786–1805.

Kent, J., 1990. *South Island Trout Fishing Guide*. Auckland ed. Reed Publishing (NZ) Ltd.: Reed Publishing (NZ) Ltd.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. and Mortensen, E., 2003. Atlantic salmon Salmo salar L., brown trout Salmo trutta L. and Arctic charr Salvelinus alpinus (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12(1), pp.1–59.

Knapp, G., Roheim, C.A. and Anderson, J.L., 2007. *The Great Salmon Run: Competition Between Wild and Farmed Salmon*. *TRAFFIC North America*, Washington DC: TRAFFIC North America (WWF).

Kongtorp, R.T., Taksdal, T. and Lyngøy, A., 2004. Pathology of heart and skeletal muscle inflammation (HSMI) in farmed Atlantic salmon Salmo salar. *Diseases of Aquatic Organisms*, 59(3), pp.217–224.

Kotler, B.T., Brown, J.S. and Hasson, O., 1991. Factors Affecting Gerbil Foraging Behavior and Rates of Owl Predation. *Ecology*, 72(6), pp.2249–2260.

Kovach, R., Jonsson, B., Jonsson, N., Arismendi, I., Williams, J., Kershner, J., Al-chokhachy, R., Letcher, B., Muhlfeld, C. and Trout, B., 2019. Climate Change and the Future of Trout and Char. In: J.L. Kershner, J.E. Williams, R.E. Gresswell and J. Lobón-Cerviá, eds. *Trout and Char of the World*. American Fisheries Society.pp.1–

32.

Lack, D., 1968. Bird Migration and Natural Selection. *Oikos*, 19(1), pp.1–9.

Lampart, W., 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology*, 3(1), pp.21–27.

Lank, D.B., Butler, R.W., Ireland, J. and Ydenberg, R.C., 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos*, 103, pp.303–319.

Lennox, R.J., Chapman, J.M., Souliere, C.M., Tudorache, C., Wikelski, M., Metcalfe, J.D. and Cooke, S.J., 2016. Themed Issue Article : Conservation Physiology of Animal Migrations Conservation physiology of animal migration. *Conservation Physiology*, 4, pp.1–15.

Letcher, B.H., Walker, J.D., O'Donnell, M.J., Whiteley, A.R., Nislow, K.H. and Coombs, J.A., 2018. Three Visualization Approaches for Communicating and Exploring Passive Integrated Transpnder Tag Data. *Fisheries*, 43(5), pp.241–248.

Liermann, C.R., Nilsson, C., Robertson, J. and Ng, R.Y., 2012. Implications of Dam Obstruction for Global Freshwater Fish Diversity. *BioScience*, 62(6), pp.539–548.

Linløkken, A.N., Johansen, W. and Wilson, R.C., 2014. Genetic structure of brown trout, Salmo trutta, populations from differently sized tributaries of Lake Mjøsa in south-east Norway. *Fisheries Management and Ecology*, 21(6), pp.515–525.

Lockard, R.B. and Owings, D.H., 1974. Moon-related surface activity of bannertail (Dipomys spectabilis) and fresno (D. nitratoides) kangaroo rats. *Animal Behaviour*, 22, pp.262–273.

Lucas, M.C., Baras, E., Thom, T.J., Duncan, A. and Slavík, O., 2001. *Migration of Freshwater Fishes*. Bodmin, Cornwall: Blackwell Sciance.

Lucas, M.C., Lucas, M.C., Baras, E. and Baras, E., 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries*, 1, pp.283–316.

Magurran, A.E., 2009. Threats to freshwater fish. *Science*, 325, pp.1215–1216.

Manhard, C. V, Joyce, J.E. and Gharrett, A.J., 2017. Evolution of phenology in a salmonid population : a potential adaptive response to climate change. *Canadian Journal of Fisheries and Aquatic Science*, 74(10), pp.1519–1527.

Marco-Rius, F., Caballero, P., Moran, P. and de Leaniz, C.G., 2013. Can migrants escape from density dependence? *Ecology and Evolution*, 3(8), pp.2524–2534.

Marschall, E.A., Mather, M.E., Parrish, D.L., Allison, G.W. and McMenemy, J.R., 2011. Migration delays caused by anthropogenic barriers: Modeling dams, temperature, and success of migrating salmon smolts. *Ecological Applications*, 21(8), pp.3014–3031.

Massa-Gallucci, A., Coscia, I., O'Grady, M., Kelly-Quinn, M. and Mariani, S., 2010. Patterns of genetic structuring in a brown trout (Salmo trutta L.) metapopulation. *Conservation Genetics*, 11(5), pp.1689–1699.

Matthews, M.A., Poole, W.R., Dillane, M.G. and Whelan, K.F., 1997. Juvenile recruitment and smolt output of brown trout (Salmo trutta L.) and Atlantic salmon (Salmo salar L.) from a lacustrine system in western Ireland. *Fisheries Research*, 31, pp.19–37.

McCormick, S.D., 2012. Smolt Physiology and Endocrinology. *Euryhaline Fishes: Fish Physiology*, 32, pp.199–251.

McCormick, S.D., Lerner, D.T., Monette, M.Y., Nieves-Puigdoller, K., Kelly, J.T.

and Björnsson, B.T., 2009. Taking it with you when you go: How perturbations to the freshwater environment, including temperature, dams, and contaminants, affect marine survival of salmon. *American Fisheries Society Symposium*, 69, pp.195–214.

McCormick, S.D., Shrimpton, J.M., Moriyama, S. and Björnsson, B.T., 2002. Effects of an advanced temperature cycle on smolt development and endocrinology indicate that temperature is not a zeitgeber for smolting in Atlantic salmon. *The Journal of experimental biology*, 205, pp.3553–3560.

McCormick, S.D., Shrimpton, J.M. and Zydlewski, J.D., 1996. Temperature effects on osmoregulatory physiology of juvenile anadromous fish. In: C. M. Wood and D.G. McDonald, eds. *Global warming: implications for freshwater and marine fish*. New York, NY: Cambridge University Press.pp.279–302.

McGinnity, P., de Eyto, E., Cross, T.F., Coughlan, J., Whelan, K. and Ferguson, A., 2007. Population specific smolt development, migration and maturity schedules in Atlantic salmon in a natural river environment. *Aquaculture*, 273(2–3), pp.257–268.

McGinnity, P., Jennings, E., DeEyto, E., Allott, N., Samuelsson, P., Rogan, G., Whelan, K. and Cross, T., 2009. Impact of naturally spawning captive-bred Atlantic salmon on wild populations: Depressed recruitment and increased risk of climate-mediated extinction. *Proceedings of the Royal Society B: Biological Sciences*, 276(1673), pp.3601–3610.

McKeown, N.J., Hynes, R.A., Duguid, R.A., Ferguson, A. and Prodöhl, P.A., 2010. Phylogeographic structure of brown trout Salmo trutta in Britain and Ireland: Glacial refugia, postglacial colonization and origins of sympatric populations. *Journal of Fish Biology*, 76(2), pp.319–347.

McLennan, D., Rush, E., Mckelvey, S. and Metcalfe, N.B., 2018. Timing of Atlantic

salmon Salmo salar smolt migration predicts successful passage through a reservoir. *Journal of Fish Biology*, 92, pp.1651–1656.

McNamara, J.M., Barta, Z., Klaassen, M. and Bauer, S., 2011. Cues and the optimal timing of activities under environmental changes. *Ecology Letters*, 14, pp.1183–1190.

Mobley, K.B., Granroth-Wilding, H., Ellmen, M., Vähä, J.-P., Aykanat, T., Johnston, S.E., Orell, P., Erkinaro, J. and Primmer, C.R., 2019. Home ground advantage: Local Atlantic salmon have higher reproductive fitness than dispersers in the wild. *Science Advances*, 5(2), pp.1–8.

Molloy, S., Holland, C. and Poole, R., 1993. Helminth parasites of brown and sea trout Salmo trutta L. from the west coast of Ireland. *Proceedings of the Royal Irish Academy - Section B Biology and Environment*, 93B(3), pp.137–142.

Moore, A., Bendall, B., Barry, J., Waring, C., Crooks, N. and Crooks, L., 2012. River temperature and adult anadromous Atlantic salmon, Salmo salar, and brown trout, Salmo trutta. *Fisheries Management and Ecology*, 19, pp.518–526.

Moore, A., Cotter, D., Quayle, V., Rogan, G., Poole, R., Lower, N. and Privitera, L., 2008. The impact of a pesticide on the physiology and behaviour of hatchery-reared Atlantic salmon, Salmo salar, smolts during the transition from fresh water to the marine environment. *Fisheries Management and Ecology*, 15(5–6), pp.385–392.

Moore, A., Ives, S., Mead, T.A. and Talks, L., 1998. The migratory behaviour of wild Atlantic salmon (Salmo salar L.) smolts in the River Test and Southampton Water, southern England. *Hydrobiologia*, 371, pp.295–304.

Moore, A., Scott, A.P., Lower, N., Katsiadaki, I. and Greenwood, L., 2003. The

effects of 4-nonylphenol and atrazine on Atlantic salmon (Salmo salar L) smolts. *Aquaculture*, 222(1–4), pp.253–263.

Morrison, D.W., 1978. Lunar phobia in a neotropical fruit bat, Artibeus jamaicensis (Chiroptera: Phyllostomidae). *Animal Behaviour*, 26, pp.852–855.

Muhlfeld, C., Dauwalter, D., D'angelo, V., Ferguson, A., Giersch, J., Impson, N., Koizumi, I., Kovach, R., Mcginnity, P., Schöffmann, J., Vøllestad, L. and Epifanio, J., 2019. Global Status of Trout and Char: Conservation Challenges in the Twenty-First Century. In: J.L. Kershner, J.E. Williams, R.E. Gresswell and J. Lobón-Cerviá, eds. *Trout and Char of the World*. American Fisheries Society.pp.717–760.

Murphy, T.M., Rodger, H.D., Drinan, E.M., Gannon, F., Kruse, P. and Korting, W., 1992. The sequential pathology of pancreas disease in Atlantic salmon farms in Ireland. *Journal of Fish Diseases*, 15(5), pp.401–408.

Music, P.A., Hawkes, J.P. and Cooperman, M.S., 2010. Magnitude and Causes of Smolt Mortality in Rotary Screw Traps: An Atlantic Salmon Case Study. *North American Journal of Fisheries Management*, 30(3), pp.713–722.

Nevoux, M., Finstad, B., Davidsen, J.G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O. and Jonsson, B., 2019. Environmental influences on life history strategies in partially anadromous brown trout (Salmo trutta, Salmonidae). *Fish and Fisheries*, 20(6), pp.1051–1082.

Northcote, T.G., 1992. Prediction and Assessment of Potential Effects of Global Environmental Change on Freshwater Sport Fish Habitat in British Columbia. *GeoJournal*, 28(1), pp.39–49.

Nosil, P., Egan, S.P. and Funk, D.J., 2008. Heterogeneous genomic differentiation

between walking-stick ecotypes: 'Isolation by adaptation' and multiple roles for divergent selection. *Evolution*, 62(2), pp.316–336.

O' Reilly, C.M., Rowley, R.J., Schneider, P., Lenters, J.D., Mcintyre, P.B., Kraemer, B.M., Weyhenmeyer, G.A., Straile, D., Dong, B., Adrian, R., Allan, M.G., Anneville, O., Arvola, L., Austin, J., Bailey, J.L., Baron, J.S., Brookes, J.D., de Eyto, E., Dokulil, M.T., Hamilton, D.P., Havens, K., Hetherington, A.L., Higgins, S.N., Hook, S., Izmest'eva, L.R., Joehnk, K.D., Kangur, K., Kasprzak, P., Kumagai, M., Kuusisto, E., Leshkevich, G., Livingstone, D.M., MacIntyre, S., May, L., Melack, J.M., Mueller-Navarra, D.C., Naumenko, M., Noges, P., Noges, T., North, R.P., Plisnier, P.-D., Rigosi, A., Rimmer, A., Rogora, M., Rudstam, L.G., Rusak, J.A., Salmaso, N., Samal, N.R., Schindler, D.E., Schladow, S.G., Schmid, M., Schmidt, S.R., Silow, E., Soylu, M.E., Teubner, K., Verburg, P., Voutilainen, A., Watkinson, A., Williamson, C.E. and Zhang, G., 2015. Rapid and highly variable warming of lake surface waters around the globe. *Geophysical research letters*, 42(24), pp.10773–10781.

O'Toole, C.L., Reed, T.E., Bailie, D., Bradley, C., Cotter, D., Coughlan, J., Cross, T., Dillane, E., Mcevoy, S., Ó Maoiléidigh, N., Prodöhl, P., Rogan, G. and McGinnity, P., 2015. The signature of fine scale local adaptation in Atlantic salmon revealed from common garden experiments in nature. *Evolutionary Applications*, 8(9), pp.881–900.

Olsen, A.B., Melby, H.P., Speilberg, L., Evensen and Håstein, T., 1997. Piscirickettsia salmonis infection in Atlantic salmon Salmo salar in Norway - Epidemiological, pathological and microbiological findings. *Diseases of Aquatic Organisms*, 31(1), pp.35–48.

Oppedal, F., Taranger, G.L., Juell, J.-E. and Hansen, T., 1999. Growth, osmoregulation and sexual maturation of underyearling Atlantic salmon smolt Salmo salar L. exposed to different intensities of continuous light in sea cages. *Aquaculture Research*, 30, pp.491–499.

Orsini, L., Vanoverbeke, J., Swillen, I., Mergeay, J. and De Meester, L., 2013. Drivers of population genetic differentiation in the wild: Isolation by dispersal limitation, isolation by adaptation and isolation by colonization. *Molecular Ecology*, 22(24), pp.5983–5999.

Otero, J., L'Abée-Lund, J.H., Castro-Santos, T., Leonardsson, K., Storvik, G.O., Jonsson, B., Dempson, B., Russell, I.C., Jensen, A.J., Baglinière, J.L., Dionne, M., Armstrong, J.D., Romakkaniemi, A., Letcher, B.H., Kocik, J.F., Erkinaro, J., Poole, R., Rogan, G., Lundqvist, H., Maclean, J.C., Jokikokko, E., Arnekleiv, J.V., Kennedy, R.J., Niemelä, E., Caballero, P., Music, P.A., Antonsson, T., Gudjonsson, S., Veselov, A.E., Lamberg, A., Groom, S., Taylor, B.H., Taberner, M., Dillane, M., Arnason, F., Horton, G., Hvidsten, N.A., Jonsson, I.R., Jonsson, N., Mckelvey, S., Næsje, T.F., Skaala, Ø., Smith, G.W., Sægrov, H., Stenseth, N.C. and Vøllestad, L.A., 2014. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (Salmo salar). *Global Change Biology*, 20(1), pp.61–75.

Ovidio, M., Baras, E., Goffaux, D., Giroux, F. and Philippart, J.C., 2002. Seasonal variation of activity pattern of brown trout (Salmo trutta) in a small stream as determined by radio-telemetry. *Hydrobiologia*, 470, pp.195–202.

Palmé, A., Laikre, L. and Ryman, N., 2013. Monitoring reveals two genetically distinct brown trout populations remaining in stable sympatry over 20 years in tiny

mountain lakes. *Conservation Genetics*, 14(4), pp.795–808.

Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D. and Reeves, G.H., 1998. Why aren't there more Atlantic salmon (Salmo salar)? *Canadian Journal of Fisheries and Aquatic Sciences*, 55, pp.281–287.

Pechmann, J.H. and Semlitsch, R.D., 1986. Diel activity patterns in the breeding migrations of winter-breeding anurans. *Canadian Journal of Zoology*, 64(5), pp.1116–1120.

Penlington, B.P., 1983. Lake-shore spawning of rainbow trout at lake Rotoma, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 17(4), pp.349–355.

Pettersen, R.A., Hytterød, S., Vøllestad, L.A. and Mo, T.A., 2013. Osmoregulatory disturbances in Atlantic salmon, Salmo salar L., caused by the monogenean Gyrodactylus salaris. *Journal of Fish Diseases*, 36(1), pp.67–70.

Plunket-Greene, H., 1924. *Where the Bright Waters Meet*. Worcester: Ebenezer Baylis Limited.

Poole, W.R., Dillane, M., Deeyto, E., Rogan, G., Mcginnity, P. and Whelan, K., 2007. Characteristics of the Burrishoole Sea Trout Population: Census, Marine Survival, Enhancement and Stock-Recruitment Relationship, 1971-2003. In: G. Harris and N. Milner, eds. *Sea Trout: Biology, Conservation and Management*. Wiley-Blackwell.pp.279–306.

Poole, W.R., Reynolds, D. and Moriarty, C., 1990. Observations on the Silver Eel Migrations of the Burrishoole River System, Ireland, 1959 to 1988. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 75(6), pp.807–815.

Poole, W.R., Whelan, K.F., Dillane, M.G., Cooke, D.J. and Matthews, M., 1996. The performance of sea trout, Salmo trutta L., stocks from the Burrishoole system western Ireland, 1970-1994. *Fisheries Management and Ecology*, 3(1), pp.73–92.

Prévost, E., Parent, E., Crozier, W., Davidson, I., Dumas, J., Gudbergsson, G., Hindar, K., McGinnity, P., MacLean, J. and Sættem, L.M., 2003. Setting biological reference points for Atlantic salmon stocks: Transfer of information from data-rich to sparse-data situations by Bayesian hierarchical modelling. *ICES Journal of Marine Science*, 60(6), pp.1177–1193.

Quinn, T.P., 1990. Current controversies in the study of salmon homing. *Ethology Ecology and Evolution*, 2(1), pp.49–63.

Quinn, T.P. and Adams, D.J., 1996. Environmental changes affecting the migratory timing of american shad and sockeye salmon. *Ecology*, 77(4), pp.1151–1162.

Quinn, T.P., McGinnity, P. and Reed, T.E., 2016. The paradox of "premature migration" by adult anadromous salmonid fishes: patterns and hypotheses. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(7), pp.1015–1030.

Quinn, T.P., Unwin, M.J. and Kinnison, M.T., 2000. Evolution of temporal isolation in the wild: Genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution*, 54(4), pp.1372–1385.

Reed, T.E., de Eyto, E., O'Higgins, K., Gargan, P., Roche, W., White, J., O'Maoileidigh, N., Quinn, T.P. and McGinnity, P., 2017. Availability of holding habitat in lakes and rivers affects the incidence of spring (premature) upriver migration by Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(5), pp.668–679.

Reed, T.E., Schindler, D.E., Hague, M.J., Patterson, D.A., Meir, E., Waples, R.S. and Hinch, S.G., 2011. Time to Evolve? Potential evolutionary responses of fraser river sockeye salmon to climate change and effects on persistence. *PLoS ONE*, 6(6).

Reed, T.E., Wanless, S., Harris, M.P., Frederiksen, M., Kruuk, L.E.B. and Cunningham, E.J.A., 2006. Responding to environmental change: Plastic responses vary little in a synchronous breeder. *Proceedings of the Royal Society B: Biological Sciences*, 273(1602), pp.2713–2719.

Richardson, J.L., Urban, M.C., Bolnick, D.I. and Skelly, D.K., 2014. Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology and Evolution*, 29(3), pp.165–176.

Riley, W.D., Potter, E.C.E., Biggs, J., Collins, A.L., Jarvie, H.P., Jones, J.I., Kelly-Quinn, M., Ormerod, S.J., Sear, D.A., Wilby, R.L., Broadmeadow, S., Brown, C.D., Chanin, P., Copp, G.H., Cowx, I.G., Grogan, A., Hornby, D.D., Huggett, D., Kelly, M.G., Naura, M., Newman, J.R. and Siriwardena, G.M., 2018. Small Water Bodies in Great Britain and Ireland: Ecosystem function, human-generated degradation, and options for restorative action. *Science of the Total Environment*, 645, pp.1598–1616.

Robertsen, G., Armstrong, J.D., Nislow, K.H., Herfindal, I., Mckelvey, S. and Einum, S., 2014. Spatial variation in the relationship between performance and metabolic rate in wild juvenile Atlantic salmon. *Journal of Animal Ecology*, 83(4), pp.791–799.

Russell, I.C., Aprahamian, M.W., Barry, J., Davidson, I.C., Fiske, P., Ibbotson, A.T., Kennedy, R.J., Maclean, J.C., Moore, A., Otero, J., Potter, T. and Todd, C.D., 2012. The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES Journal of Marine*

Science, 69(9), pp.1563–1573.

Rustadbakken, A., L'Abee-Lund, J.H., Arnekleiv, J.V., Kraabøl, M., L'Abée-Lund, J.H., Arnekleiv, J.V. and Kraabøl, M., 2004. Reproductive migration of brown trout in a small Norwegian river studied by telemetry. *Journal of Fish Biology*, 64, pp.2–15.

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. and van Bommel, F.P.J., 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, 131(1), pp.93–105.

Sandlund, O.T., Diserud, O.H., Poole, R., Bergesen, K., Dillane, M., Rogan, G., Durif, C., Thorstad, E.B. and Vøllestad, L.A., 2017. Timing and pattern of annual silver eel migration in two European watersheds are determined by similar cues. *Ecology and Evolution*, 7(15), pp.5956–5966.

Sandlund, O.T. and Jonsson, B., 2016. Life history plasticity: Migration ceased in response to environmental change? *Ecology of Freshwater Fish*, 25(2), pp.225–233.

Sawyer, F., 1970. *Nymphs and the Trout*. London: A & C Black Publishers Ltd.

Scanes, E., Scanes, P.R. and Ross, P.M., 2020. Climate change rapidly warms and acidifies Australian estuaries. *Nature Communications*, 11(1), pp.1–11.

Schindler, D.E., 2019. The phenology of migration in an unpredictable world. *Journal of Animal Ecology*, 88(8), pp.8–10.

Schindler, D.E., Armstrong, J.B. and Reed, T.E., 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, 13(5), pp.257–263.

Schwinn, M., Aarestrup, K., Baktoft, H. and Koed, A., 2017. Survival of Migrating

Sea Trout (Salmo trutta) Smolts During Their Passage of an Artificial Lake in a Danish Lowland Stream. *River Research and Applications*, 33(4), pp.558–566.

Schwinn, M., Baktoft, H., Aarestrup, K. and Koed, A., 2019. Artificial lakes delay the migration of brown trout Salmo trutta smolts: a comparison of migratory behaviour in a stream and through an artificial lake. *Journal of Fish Biology*, 94, pp.745–751.

Scranton, K. and Amarasekare, P., 2017. Predicting phenological shifts in a changing climate. *PNAS*, 114(50), pp.11312–11317.

Seebacher, F. and Post, E., 2015. Climate change impacts on animal migration. *Climate Change Responses*, 2, pp.5–6.

Shaw, A.K., 2016. Drivers of animal migration and implications in changing environments. *Evolutionary Ecology*, 30, pp.991–1007.

Shephard, S. and Gargan, P., 2017. Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. *Aquaculture Environment Interactions*, 9, pp.181–192.

Shephard, S., MacIntyre, C. and Gargan, P., 2016. Aquaculture and environmental drivers of salmon lice infestation and body condition in sea trout. *Aquaculture Environment Interactions*, 8, pp.597–610.

Skalski, J.R., Smith, S.G., Iwamoto, R.N., Williams, J.G. and Hoffmann, A., 1998. Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(1981), pp.1484–1493.

Slavík, O., Horký, P., Randák, T., Balvín, P. and Bílý, M., 2012. Brown Trout

Spawning Migration in Fragmented Central European Headwaters : Effect of Isolation by Artificial Obstacles and the Moon Phase. *Transactions of the American Fisheries Society*, 141, pp.673–680.

Stabell, O.B., 1984. Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon. *Biological Reviews*, 59(3), pp.333–388.

Staurnes, M., Sigholt, T., Asgard, T. and Baeverfjord, G., 2001. Effects of a temperature shift on seawater challenge test performance in Atlantic salmon (Salmo salar) smolt. *Aquaculture*, 201, pp.153–159.

Strayer, D.L. and Dudgeon, D., 2010. Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society*, 29(1), pp.344–358.

Sutherland, D.R. and Predavec, M., 1999. The effects of moonlight on microhabitat use by Antechinus agilis (Marsupialia : Dasyuridae). *Australian Journal of Zoology*, 47, pp.1–17.

Swatdipong, A., Vasemägi, A., Niva, T., Koljonen, M.L. and Primmer, C.R., 2010. High level of population genetic structuring in lake-run brown trout, Salmo trutta, of the Inari Basin, northern Finland. *Journal of Fish Biology*, 77(9), pp.2048–2071.

The_Standing_Scientific_Committee_on_Salmon, 2016. *Independent Scientific Report to Inland Fisheries Ireland: The Status of Irish Salmon Stocks in 2010, with Precautionary Catch Advice for 2011*.

Thorstad, E.B. and Finstad, B., 2018. *Impacts of salmon lice emanating from salmon farms on wild Atlantic salmon and sea trout*. *NINA Report*, .

Thorstad, E.B., Todd, C.D., Uglem, I., Bjørn, P.A., Gargan, P.G., Vollset, K.W.,

Halttunen, E., Kålås, S., Berg, M. and Finstad, B., 2015. Effects of salmon lice Lepeophtheirus salmonis on wild sea trout salmo trutta - A literature review. *Aquaculture Environment Interactions*, 7(2), pp.91–113.

Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H. and Finstad, B., 2012. A critical life stage of the Atlantic salmon Salmo salar: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81(2), pp.500–542.

Tierney, K.B., Sampson, J.L., Ross, P.S., Sekela, M.A. and Kennedy, C.J., 2008. Salmon olfaction is impaired by an environmentally realistic pesticide mixture. *Environmental Science and Technology*, 42(13), pp.4996–5001.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D. and Swackhamer, D., 2001. Forecasting Agriculturally Driven Global Environmental Change. *Science*, 292, pp.281–284.

Todd, C.D., Friedland, K.D., Maclean, J.C., Hazon, N. and Jensen, A.J., 2011. Getting into hot water? Atlantic salmon responses to climate change in freshwater and marine environments. In: Ø. Aas, A. Klemetsen, S. Einum and J. Skurdal, eds. *Atlantic Salmon Ecology*. Wiley.pp.409–443.

Tully, O. and Whelan, K.F., 1993. Production of nauplii of Lepeophtheirus salmonis (Krøyer) (Copepoda: Caligidae) from farmed and wild salmon and its relation to the infestation of wild sea trout (Salmo trutta L.) off the west coast of Ireland in 1991. *Fisheries Research*, 17(1–2), pp.187–200.

Wanstall, S.T., Robotham, P.W.J. and Thomas, J.S., 1986. Pathological changes induced by Pomphorbynchus laevis Muller (Acanthocephala) in the gut of rainbow

trout, Salmo gairdneri Richardson. *Parasitenkunde*, 72, pp.105–114.

Wanstall, S.T., Thomas, J.S. and Robotham, P.W.J., 1988. The pathology caused by Pomphorhynchus laevis Muller in the alimentary tract of the stone loach, Noemacheilus harbatulus (L.). *Journal of Fish Diseases*, 11, pp.511–523.

Whelan, K., 2010. *A Review of the Impacts of the Salmon Louse, Lepeophtheirus salmonis (Krøyer, 1837) on Wild Salmonids*. *Atlantic Salmon Trust*, Perth.

Whelan, K.F., Poole, W.R., McGinnity, P., Rogan, G. and Cotter, D., 1998. The Burrishoole System. In: *Studies of Irish Rivers and Lakes, Essays on the occasion of the XXVII Congress of Societas Internationalis Limnologiae (SIL)*. Dublin.pp.191–212.

Whittow, J.B., 1974. *Geology and scenery in Ireland*. England: Pelican Books.

Wilcove, D.S., 2008. *No Way Home: The Decline of the World's Great Animal Migrations*. Washington: Island Press.

Wilcove, D.S. and Wikelski, M., 2008. Going , Going , Gone : Is Animal Migration Disappearing? *PLoS Biology*, 6(7), pp.1361–1364.

Williams, C., Barnes, B. and Buck, C.L., 2014. Phenology of hibernation and reproduction in ground squirrels: integration of environmental cues with endogenous programming. *Journal of Zoology*, 29(2), pp.112–124.

Winkler, D.W., Jørgensen, C., Both, C., Houston, A.I., McNamara, J.M., Levey, D.J., Partecke, J., Fudickar, A., Kacelnik, A., Roshier, D. and Piersma, T., 2014. Cues, strategies, and outcomes: How migrating vertebrates track environmental change. *Movement Ecology*, 2(1), pp.1–15.

Winter, E.R., Tummers, J.S., Aarestrup, K., Baktoft, H. and Lucas, M.C., 2016.

Investigating the phenology of seaward migration of juvenile brown trout (Salmo trutta) in two European populations. *Hydrobiologia*, 775(1), pp.139–151.

Woolway, R.I., Weyhenmeyer, G.A., Schmid, M., Dokulil, M.T., de Eyto, E., Maberly, S.C., May, L. and Merchant, C.J., 2019. Substantial increase in minimum lake surface temperatures under climate change. *Climatic Change*, 155(1), pp.81–94.

Youngson, A.F., Buck, R.J.G., Simpson, T.H. and Hay, D.W., 1983. The autumn and spring emigrations of juvenile Atlantic salmon, Salmo salar L., from the Girnock Burn, Aberdeenshire, Scotland: environmental release of migration. *Journal of Fish Biology*, 23(6), pp.625–639.

Zydlewski, G.B., Haro, A., Whalen, K.G. and McCormick, S.D., 2001. Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. *Journal of Fish Biology*, 58(5), pp.1471–1475.

Zydlewski, G.B., Horton, G., Dubreuil, T., Letcher, B., Casey, S. and Zydlewski, J., 2006. Remote monitoring of fish in small streams. *Fisheries Research*, 31(9), pp.433–446.

Zydlewski, G.B., Stich, D.S. and Mccormick, S.D., 2014. Photoperiod control of downstream movements of Atlantic salmon Salmo salar smolts. *Journal of Fish Biology*, 85(4), pp.1023–1041.

Zydlewski, J., Zydlewski, G. and Danner, G.R., 2010. Descaling Injury Impairs the Osmoregulatory Ability of Atlantic Salmon Smolts Entering Seawater. *Transactions of the American Fisheries Society*, 139(1), pp.129–136.

Chapter 2

Hyper- and hypo-osmoregulatory performance of Atlantic salmon (*Salmo salar*) smolts infected with *Pomphorhynchus laevis* (Acanthocephala)

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Author Contributions: RF, TR, and RP conceived and designed the experiment. RF, RP and GR collected the data. RF and TR analysed the data. RF wrote the first draft of the manuscript. All authors contributed to drafts of the manuscript and gave final approval for publication.

Abstract

The shift from freshwater to marine environments that defines anadromous fishes requires complex changes in many organs involved in osmoregulation, including the intestines. Consequently, any reduction in intestinal function might compromise adaptation to marine waters. The Irish freshwater strain of the acanthocephalan parasite *Pomphorhynchus laevis* uses salmonids rather than cyprinids as preferred definitive hosts, perforating the intestines, destroying mucosa and inducing inflammation. We investigated whether infection intensities of *P. laevis* in wild Atlantic salmon (*Salmo salar* L.) smolts were associated with reduced osmoregulatory performance, as measured by plasma chloride concentrations, or elevated stress, as measured by blood glucose and plasma cortisol, in freshwater or saltwater environments. Three groups (n = 66 smolts per group) were captured at sea entry and held for either 24 h in fresh water, 24 h in salt water or 72 h in salt water, after which blood was sampled and individual infection intensity of *P. laevis* was recorded. Although infection prevalence was high amongst experimental samples, no associations were found within or across treatment groups between individual infection intensity and the physiological parameters. We found no vacant intestinal perforations that would indicate *P. laevis* had recently vacated the intestines of smolts sampled in either of the saltwater groups. Exploratory sampling in the two years preceding the experiment indicated that infection prevalence and intensity in this Atlantic salmon population are consistently high and comparable to the experimental samples. Collectively, these results indicate that naturally-occurring infection intensities of *P. laevis* in Irish salmon do not cause stress or reduced osmoregulatory function in fresh water or immediately after entering salt water. However, delayed pathologies affecting marine survival may occur, particularly if

intestinal perforations vacated by *P. laevis* allow ingress of liquids into the peritoneum.

Introduction

The life histories of anadromous species such as Atlantic salmon (*Salmo salar* L.) or Pacific salmonids (*Onchorynchus* spp.) necessitate the regulation of internal osmotic balance in hypoosmotic (freshwater) and hyperosmotic (saltwater) environments. In fresh water, osmoregulation requires excess water, which is passively absorbed through osmosis across the gills and skin, to be excreted as dilute urine (Genz, Esbaugh and Grosell, 2011). In contrast, osmoregulation in a marine environment requires salmon to continuously drink salt water and actively uptake H_20 through the intestinal epithelium into the body while limiting intestinal absorption of ions in order to mitigate diffusive water losses through the gills and skin (Grosell, 2007; Whittamore, 2012). The initial period of acclimation to the marine environment therefore necessitates significant changes to the internal physiology of salmon smolts (Stefansson et al., 2012) and provides an acute physiological challenge (Handeland et al., 2014). Plasma cortisol levels rise during the parr-smolt transformation, and this natural stress response is thought to benefit smolts by mobilizing energy reserves and increasing saltwater tolerance (Bisbal and Specker, 1991; Strand and Finstad, 2007). However, further sources of acute or chronic stress can greatly impair osmoregulatory ability in salmonid smolts (Redding and Schreck, 1983; Iversen, Finstad and Nilssen, 1998) as observed with infestations of ectoparasitic sea lice (*Lepeophtheirus salmonis*) (Poole, Nolan and Tully, 2000) or *Gyrodactylus salaris* (Bakke and Harris, 1998). Parasite-induced damage to organs involved in osmoregulation such as the skin, gills or intestines can also directly impact the

ability of salmonids to maintain osmotic homeostasis in salt water, leading to disruption of physiological processes, elevated stress, and ultimately mortality (Wells et al., 2006; Finstad et al., 2012; Dawson et al., 1998; Hvas et al., 2017). Through these pathological effects, increased sea lice infestations associated with fish farming are regarded as a significant factor contributing to declines in the marine survival of many Atlantic salmon and sea trout (anadromous *Salmo trutta* L.) stocks in recent decades (Poole et al., 2007; Shephard and Gargan, 2017; Thorstad et al., 2015; Krkošek et al., 2013).

Pomphorhynchus laevis is an acanthocephalan endoparasite of various freshwater and brackish fishes with a complex (heteroxenous) life cycle that requires infection of both intermediate and definitive host species. Gammarid species are used as intermediate hosts and trophic transmission to a definitive host requires the consumption of an infected gammarid by a suitable fish species (Perrot-Minnot, Bollache and Lagrue, 2020). Upon consumption by a salmonid, *P. laevis* use their hooked proboscis to pierce all layers of the intestinal wall and anchor themselves in place. This process creates a perforation leading from the interior to the exterior of the intestinal wall, destroying intestinal mucosa, causing a localised inflammatory response and potentially altering the physiological performance of the intestine in controlling transepithelial ion transport (Wanstall, Thomas and Robotham, 1988; Dezfuli et al., 2008; Wanstall, Robotham and Thomas, 1986; Dezfuli et al., 2002b). Previous studies have concluded that, despite causing such intestinal damage, infection with *P. laevis* does not significantly reduce growth rates in salmonids and does not directly cause mortality of the host (Wanstall, 1984; Wanstall, Robotham and Thomas, 1986; Hine and Kennedy, 1974). However, these studies have focused on the impact of *P. laevis* infection on salmonids in fresh water where

osmoregulation does not require equivalent control of transepithelial ion transport or active H_20 uptake through the intestinal wall as is necessary in saltwater environments.

P. laevis has a discontinuous geographical distribution, stretching from the Baltic sea to north western coastlines of Europe, with isolated records from outside this range (Hohenadler et al., 2018; Roohi, Pazooki and Sattari, 2015; Kennedy, Bates and Brown, 1989). Its distribution in Britain is comparatively restricted while it is widespread in Ireland (Hine and Kennedy, 1974). Irish and English freshwater strains have been identified, as well as a marine strain that is found in coastal British waters, all of which appear to have diverged relatively recently (Kennedy, Bates and Brown, 1989; Munro, Reid and Whitfield, 1990; O'Mahony et al., 2004; O'Mahony, Kennedy and Holland, 2004). Furthermore, each strain exhibits differing morphological characteristics and is associated with different preferred intermediate and definitive hosts (O'Mahony, Kennedy and Holland, 2004; Munro, Whitfield and Diffley, 1989; Guillen-Hernandez and Whitfield, 2001). Cyprinids and flounder (*Platichthys flesus*) tend to be the preferred definitive hosts of the English freshwater and marine strains respectively, while salmonids and are regarded as the preferred hosts of the Irish freshwater strain (Molloy, Holland and O'Regan, 1995; Ziolkowska et al., 2000; O'Mahony et al., 2004). Indeed, Pippy (1969a) found that the incidence of *P. laevis* in Atlantic salmon smolts in Ireland was 25 times higher than in Scotland, England and Wales. Previous Irish studies found that *P. laevis* infection rates of brown trout peaked in spring, coinciding with the annual smolt run (Molloy, Holland and O'Regan, 1995), and that smolt-aged salmon (i.e. 2+) tend to carry the highest infection intensities (Fitzgerald and Mulcahy, 1983). Thus,

anadromous salmonids in Ireland have a particularly high chance of entering salt water while infected by *P. laevis*.

Exposure to sub-optimal conditions or stressors in fresh water has been shown to reduce osmoregulatory performance and increase the susceptibility of salmonids to parasitic infection and associated mortality in the marine environment (Finstad et al., 2012, 2007). In the present study, we sought to investigate whether the natural freshwater infection intensities of *P. laevis* found in wild Irish Atlantic salmon smolts affected osmoregulatory performance or stress in saltwater or freshwater environments. We hypothesised that perforations made by *P. laevis* in the intestinal wall would allow uncontrolled ingress of water into the peritoneum while parasite-induced damage to mucosa, and the associated inflammatory response, would further reduce the ability of salmonids to control ion uptake or water absorption through the intestines. Through these processes, *P. laevis* infection was predicted to compromise the osmoregulatory performance of Atlantic salmon in salt water, leading to elevated stress and increased ion concentrations in the blood. We characterised infection prevalence and intensities of wild smolts captured from the Burrishoole catchment, Co. Mayo, over a three-year period and investigated whether infection patterns were associated with variation in fish size, sex or condition. Smolts captured on the third year were held in fresh (n = 66) or salt (n= 132) water prior to sampling and blood samples were extracted shortly after euthanasia. We then used measurements of plasma cortisol concentrations and blood glucose levels as reliable indicators of physiological stress (Martinez-Porchas, Martinez-Cordova and Ramos-Enriquez, 2009) and plasma chloride concentrations as a direct measure of internal osmotic balance (McCormick, 2012) and, therefore, osmoregulatory performance. Using these data, we investigated whether *P. laevis* number was associated with variation

in stress levels or osmoregulatory performance of smolts in fresh or salt water environments.

Methods

Exploratory sampling

Wild Atlantic salmon smolts that had been captured for stock assessment purposes at the tidal limit of the Burrishoole river system (NW Ireland) in May 2016 (n = 136) and May 2017 (n = 39) were dissected and their digestive tracts were inspected for the presence of acanthocephalan parasites. Attached and unattached acanthocephalans were recorded and identified to species level by inspection of the praesoma under a microscope (morphological characteristics described by O'Mahony et al., (2004)). Smolt weight (to 0.1g) and fork length (to 1 mm) were recorded before dissection and sex was determined by inspection of gonads during removal of the digestive tract. Chi-square and Mann-Whitney U tests were used to investigate whether there was a significant relationship between infection prevalence or infection intensity, respectively, and sex amongst the smolts sampled in 2016, 2017 or amongst the experimental 2018 samples.

Experimental setup

On two occasions during 2018, emigrating wild smolts (mean fork length = 138.9 mm, SD = 9.5 mm, range = 121 – 168 mm) were captured at the Salmon Leap fish trap located at the confluence between the Burrishoole river system and the saline environment of Lough Furnace and Clew Bay. On each occasion, captured smolts were transported < 100 m to an indoor Marine Institute research facility where they

were transferred in an ad hoc fashion to evenly populate four 500 L aerated experimental tanks. On the first capture occasion (02 May), 66 smolts were distributed evenly amongst four tanks that had each been filled with 300 L of fresh water (i.e. 16 – 17 smolts per tank). After 24 hours all 66 smolts were terminally sampled (see next section), at which point the experiment finished for this freshwater treatment group (24FW) and the four tanks were emptied of water. On the second capture occasion (05 May), 132 smolts were distributed evenly amongst the same four tanks, each now pre-filled again with 50 L of fresh water (i.e. 33 smolts per tank). During the two hours after the 132 smolts were transferred, 300 L of locally-sourced sea water were gradually added to each tank, raising the salinity in each tank to 26.1-26.3 PPT at a rate that reflects the natural salinity increase experienced by wild smolts moving from the Burrishoole system to coastal waters. Twenty-four h after the salinity had reached this peak, 66 smolts (16 – 17 smolts per tank) were terminally sampled and this group then comprised the 24 h in saltwater (24SW) treatment group. The remaining 66 smolts were then terminally sampled 48 h later, i.e. after a total of 72 h in saltwater (72SW). Water temperatures ranged between 8.4 and 13.9 °C and dissolved oxygen was maintained at > 8.5 mg/L during all phases of the experiment. The tanks were covered throughout the experiment in order to reduce exposure to potential external sources of stress.

Experimental sampling procedure

At each sampling time (i.e. 24FW, 24SW and 72SW), dip nets were used to transfer 16 – 17 smolts from each of the four tanks into a pH buffered solution of tricaine methane-sulfonate (450mg L^{-1}) while minimising disturbance to the remaining fish. Smolts were monitored until opercular movement ceased and death was confirmed

by severing the spinal cord with a scalpel (completing the killing of the animal in accordance with Annex IV of EU Directive 2010/63/EU and SI 5432 of 2012). Blood samples were extracted from the caudal vein (along midline just posterior of the anal fin) with 1 ml 21G lithium-heparinised syringes (containing ~ 6 USP units of lithium-heparin and providing ~ 15 USP units per ml of blood) immediately after cervical dislocation and transferred to 1 ml Eppendorf © tubes which were stored on ice. Mean duration between dip netting and blood sampling was nine minutes and twenty-four seconds (SD = 261 seconds).

Sample processing

A commercially available meter (FreeStyle Lite: Abbott) was used to measure the blood glucose level (mmol/L) of each fish within one minute of sacrifice. This meter has been shown to accurately measure glucose levels in teleosts (Eames et al., 2010). Each fish was then weighed (to 0.1 g), measured (fork length 'FL' to 1 mm), and a ~ 2 mm^2 clip of caudal tissue was stored in ethanol for genetic sex determination. The condition factor (Fulton's *K*) for each fish was then calculated by the following formula (Ricker, 1975):

$$K = \frac{W}{FL^3} \times 100,$$

where *K* is condition factor, W is fish weight (g) and FL is fork length (cm).

Carcasses were placed in individual sealable plastic bags and stored on ice until dissection. All fish were dissected within eight hours of mortality. An incision was made along the midventral line and the alimentary tract was removed after severing its junctures with the anus and the oesophagus. The phenotypic sex of each fish was

determined by visual inspection of the gonads and in any case where the designation was uncertain genetic methods were used to verify sex (as per Finlay et al., (2020)).

Once removed from the body, the alimentary tract of each fish was temporarily filled with water and pinched at each end to create water tight seals. The oesophageal end was then compressed to pressurise the internal water and the external wall was closely inspected for 'pinprick' leaks that would indicate the presence of unplugged perforations left by previously attached *P. laevis.* The alimentary tract was then opened by mesial incision with a fine-point scissors and divided into four sections; 1: stomach (oesophagus to pyloric caecae), 2: anterior intestine (33% of intestinal length from post-pyloric caecae to rectum); 3: intermediate intestine (middle 33% of intestine), and 4: posterior intestine (last 33% of intestine ending at anus). Each section was examined for the presence of *P. laevis* and the number of attached and unattached *P. laevis* in each section was recorded. On each sampling date, 30 *P. laevis* were examined under a microscope within 15 minutes of opening the digestive tract and their status as 'alive' or 'dead' was determined based on the presence or absence of observable movement in response to physical stimulus. A subset of *P. laevis* (n = 264) were also weighed in groups of 2-32 individuals (each group collected from a single fish) and mean individual *P. laevis* weight per group and in total were calculated. We calculated the prevalence of infection as the percentage of smolts containing *P. laevis* and the mean intensity of infection as the mean number of *P. laevis* in infected individuals.

Plasma was separated from all blood samples within four hours of extraction by spinning in a centrifuge (ALC PK 421) at 3000 rpm for ten minutes. Roughly 0.07 ml of plasma was extracted from each sample with an adjustable micropipette (Nichipet Ex) and stored in a 0.5 ml tube at – 20 °C for chloride analysis. The

remaining plasma was added to 1 ml tubes containing ~ 0.1 mg of a D4 isotopically labelled cortisol internal standard (ISTD) solution, weighed, and stored at - 20 °C for cortisol analysis. Plasma cortisol concentrations were measured with a gas chromatography-mass spectrometer (GC-MS) after first using the relationship between response ratio of cortisol/D4 cortisol and the concentration ratio of cortisol/D4 in eight stock solutions to generate a calibration curve. Results were corrected for variation in the ratio of plasma weight to ISTD weight of each sample. Plasma chloride was measured by coulometric titration using a Jenway PCLM3 chloride meter. Where plasma quantities were sufficient, chloride samples were tested in duplicate, and triplicates were run for samples showing a difference greater than three units between the first two replicates. All blood assays were conducted within three weeks of freezing plasma.

Ethical note

We adhered to the ASAB/ABS Guidelines for the Use of Animals in Research throughout this project. All actions relating to the capture and sampling of smolts as well as the manipulation of environmental salinity were carried out in accordance with S.I. No.123/2014 Animal Health and Welfare (operations and procedures) Regulations 2014 and with approval of the Marine Institute animal welfare committee (MI Establishment Authorisation No: AE19121) and the Health Professionals Regulatory Authority (HPRA Classification Request Number: 066). Procedures for euthanasia were appropriate for salmonids (Popovic et al., 2012). Sampling was carried out by personnel with appropriate training and Individual Authorisations under Scientific Animal Protection Legislation (HPRA).

Statistical analyses

We conducted all analyses using the statistical computing software R v3.6.1 (R Core Team, 2018). We specified separate generalised least squares models (GLS) using the *gls* function in the *nlme* package (J et al., 2019) to investigate the extent to which variation in blood parameters (blood glucose, plasma chloride and plasma cortisol) was associated with variation in two continuous (*P. laevis* count and fish condition factor measured as Fulton's K) and four categorical (treatment group, sex, operator and tank) explanatory variables. Treatment group had three levels (24FW, 24SW and 72SW) corresponding with the three sampling dates. Operator, with two levels designating the two operators who performed the blood sampling, was included to control for potential variation in response variables resulting from differences in sampling technique among personnel. Tank had four levels reflecting the four experimental water tanks and sex had two levels, male and female. GLS models were used in order to account for differences in the variance of each of the three response variables observed amongst the three treatment groups, i.e. to control for heteroscedasticity. For the cortisol model, the response variable was natural logarithm transformed in order to normalise the residuals as there was right skew to the raw values. Initial models included an interaction between PL and treatment group in order to test whether any effect of *P. laevis* infection on blood glucose, chloride or cortisol depended on treatment group. Models excluding this interaction were then run in order to test whether *P. laevis* infection was associated with variation in these blood parameters independently of treatment group. AIC values were used to compare models including and excluding the interaction between *P. laevis* and treatment group.

We used the *glmmTMB* function (Brooks et al., 2017) to specify generalised linear models (GLMs) to explore the degree to which the variation in infection prevalence and individual infection intensity was associated with variation in the condition factor (Fulton's K), length, weight and sex of smolts sampled in 2016, 2017 and 2018 (n = 312, the subset for which sex and size were both recorded). The individual infection intensity model included only smolts that were infected. We used negative binomial models with log link functions to investigate individual infection intensity, in order to account for residual overdispersion in the data, and binomial models with logit link functions to investigate infection prevalence. Due to high collinearity between fork length and weight ($R^2 = 0.91$), two models were specified for each response variable (i.e. infection prevalence and intensity), each including either fork length or weight, and AIC values were used to compare both models. As both the infection prevalence and infection intensity models containing fork length yielded marginally lower AIC values than the models containing weight (-0.4 and -0.6 respectively), only results from the models with fork-length are presented.

Prior to model fitting**,** collinearity between all continuous explanatory variables in each model was explored by Pearson's R with the *cor.test* function in the *stats* package and associations between continuous and categorical explanatory variables were examined visually. Variance inflation factors (VIFs) were calculated for all fixed effects in each GLM with the *check_collinearity* function in the *performance* package in R (Lüdecke et al., 2019). We tested for heteroscedasticity and violations of linearity amongst residuals from the GLMs by plotting fitted values against simulated (scaled) residuals with the *DHARMa* package (Hartig, 2019). We tested for temporal autocorrelation with the *acf* function in the *stats* package. The *qqnorm* and *plot* functions were used to investigate residual distributions from GLS models.

Chi-square tests were used to investigate whether there were significant differences in infection intensity or prevalence amongst experimental treatment groups or amongst tanks within each treatment group.

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Results

Parasite prevalence, infection intensity and locations within the alimentary tract

P. laevis infection prevalences amongst smolts sampled in 2016, 2017 and 2018 (2018 samples corresponding with the 198 smolts used in the experiment) were 74.2 %, 65.1 %, and 66.2%, respectively. Mean infection intensities amongst the 2016, 2017 and 2018 samples respectively were 9.23, 7.28 and 6.9 acanthocephalans per infected fish. Infection prevalence amongst males and females respectively was 76% and 75% in 2016 ($X^2 = 0.77$, p= 0.68), 93% and 41% in 2017 ($X^2 = 11.82$, p= 0.003) and 71% and 63% in 2018 (Chi-square: $x^2 = 0.84$, p= 0.358). Mean infection intensity per infected fish amongst males and females respectively was 12.8 and 4.9 in 2016 (Mann-Whitney U test: W = 1171, p = 0.044), 7.9 and 7.0 in 2017 (Mann-Whitney U test: W = 53.5, p = 0.416) and 6.0 and 7.6 in 2018 (Mann-Whitney U test: W = 2063, p = 0.942). Ten of the 198 smolts sampled in 2018 contained unattached *P. laevis* with nine of these smolts also containing attached *P. laevis*. A total of 899 attached and 15 unattached *P. laevis* were recorded amongst the 2018 experimental samples and the number of attached worms per fish ranged from 1 to 42 (Fig. 1).

Almost all (93.64 %) attached *P. laevis* were in the intermediate (central 33%) section of the intestine while 3.11 % and 3.25 % were located in the anterior and posterior sections respectively. No attached or unattached *P. laevis* were found in the oesophagus, stomach or pyloric caecae. A few (n = 7) *P. laevis* were attached to the muscle along the inside wall of the peritoneal cavity, having presumably passed completely through the wall of the digestive tract (Fig. 2 A). The mean weight of individual attached worms was 3.1 mg (SD of mean individual weight per smolt = 0.0015 mg). All worms from all treatment groups that were observed under a

microscope directly after removal from the intestines were found to be alive. Infection prevalence in the 24FW, 24SW and 72SW treatment groups were 63 %, 60 % and 77 % respectively (Chi-square: x^2= 6.7, p = 0.036). Mean *P. laevis* counts per fish in the 24FW, 24SW and 72SW treatment groups were 4.29, 3.48 and 5.88 respectively (Chi-square: x^2= 40.5, p= 0.769). *P. laevis* prevalence did not differ significantly amongst the four tanks in the 24FW (Chi-square: x^2 = 4.8, p = 0.183), 24SW (Chi-square: x^2 = 6.7, p = 0.084) or 72SW (Chi-square: x^2 = 0.8, p = 0.841) treatment groups. *P. laevis* count did not differ significantly amongst the four tanks in the 24FW (Chi-square: x^2 = 53.1, p = 0.507), 24SW (Chi-square: x^2 = 43.9, p = 0.390) or 72SW (Chi-square: x^2 = 49.3, p = 0.657) treatment groups.

No evidence of damage to intestine walls (i.e. pinprick leaks or visible perforations) from recently expelled *P. laevis* was observed in sampled smolts. Additionally, no leakage was observed through intestinal perforations that were plugged by the probosces of *P. laevis.* No mortality of smolts occurred in any treatment group prior to sampling. The binomial model revealed a significant positive association between infection prevalence and Fulton's K (p = 0.012) (Fig. 3 A) but no evidence of significant associations with sex or fork length (Table 1). The negative binomial model revealed a significant association between infection intensity and sex, with males having higher intensities than females (p = 0.043). This model also revealed a non-significant positive association between Fulton's K and infection intensity (p = 0.09) (Fig. 3B).

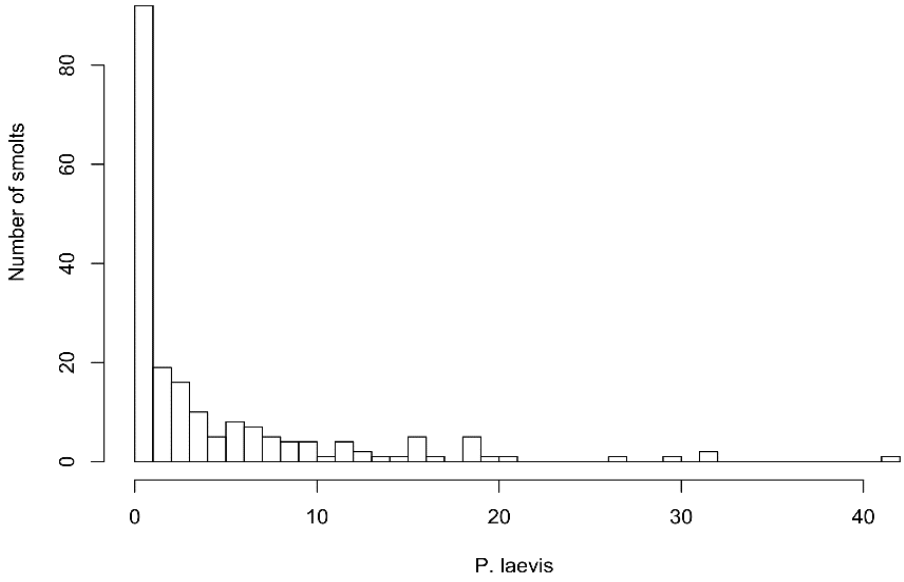


Figure 1. Histogram of *P. laevis* abundance for all smolts used in experiment (n = 198).

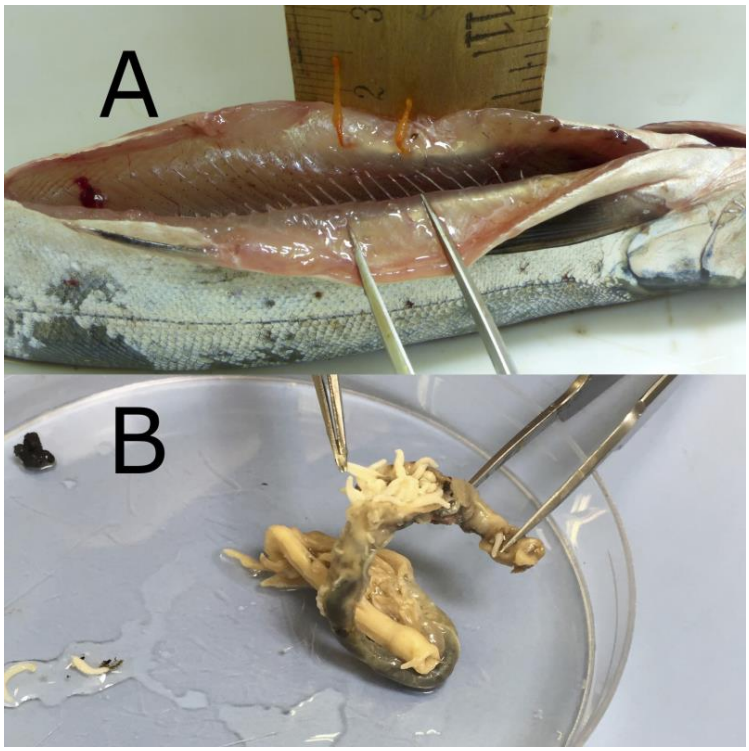


Figure 2. (A) Photograph of *P. laevis* outside the alimentary tract of salmon smolt and attached to the peritoneum and muscle wall. (B) Salmon smolt intestine, heavily infected by *P. laevis*.

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Table 1. Parameter estimates for the binomial prevalence GLM where individual infection status (i.e. infected or uninfected) is the binary response variable. The intercept corresponds to the estimates (on the logit scale) for females.

	Estimate	Std. Error	z value	p value
(Intercept)	-3.212	2.793	-1.150	0.250
Fultons' K	5.339	2.113	2.527	0.012
Fork Length	-0.054	0.126	-0.426	0.670
Sex: Male	0.252	0.255	0.990	0.322

Table 2. Parameter estimates for the negative binomial GLM where individual infection intensity (i.e. the number of *P. laevis* per fish) is the response variable. The intercept corresponds to the estimates (on the log scale) for females.

	Estimate	Std. Error	z value	p value
(Intercept)	-1.338	1.497	-0.893	0.372
Fultons' K	2.030	1.201	1.690	0.091
Fork Length	0.104	0.063	1.640	0.101
Sex: Male	0.276	0.137	2.023	0.043

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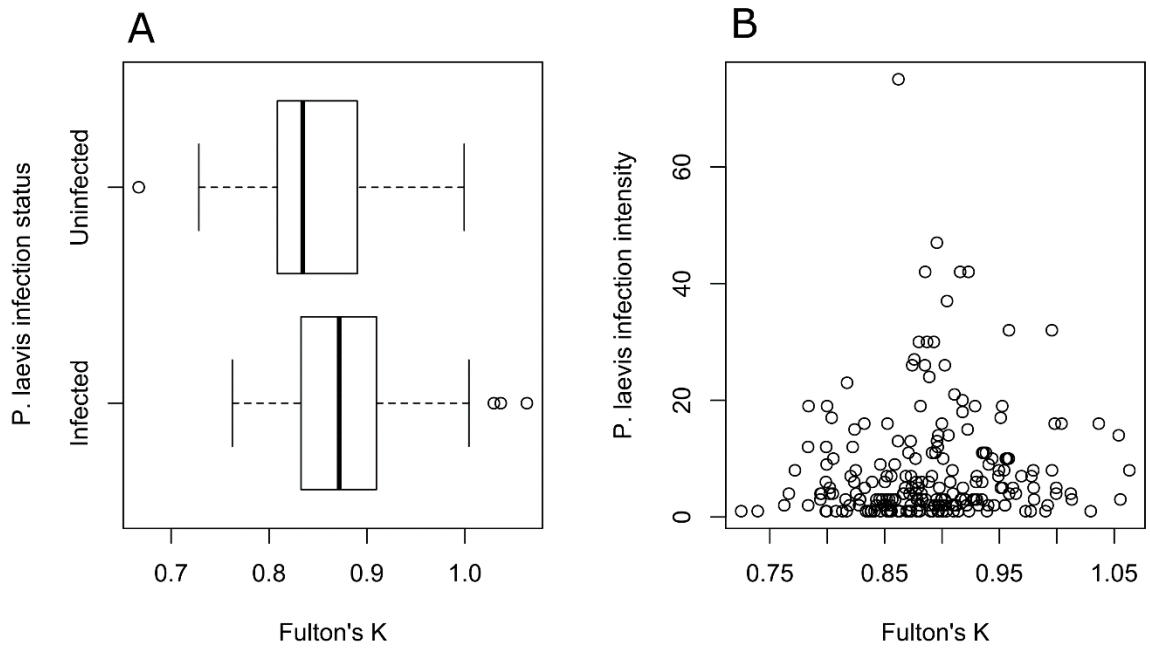


Figure 3. (A) Boxplot of infection status (i.e. whether individual smolts contain *P. laevis* or not) vs Fulton's K (condition factor) (n = 312) and (B) scatterplot of individual infection intensity (i.e. the number of *P. laevis* per infected smolt) vs Fulton's K (n = 218). Data include smolts sampled in 2016, 2017 and 2018.

Blood parameters

The mean blood parameters in each treatment group fell within reported ranges for Atlantic salmon (Table 3) (Kolarevic et al., 2014; Finstad et al., 2012; Bowers et al., 2000). Our initial chloride model revealed no significant interaction between *P. laevis* count and treatment group ($p = 0.447$). When this interaction was excluded, the model AIC value decreased by ~ 7 and the main effect of *P. laevis* count was non-significant ($p = 0.26$) (Fig.4). The model without an interaction revealed significantly higher plasma chloride concentrations in the 24SW and 72SW treatment groups relative to the 24FW group (Table 3 and Table 4). This model also revealed a significant negative

relationship between Fulton's K and plasma chloride (Table 4). However, *P. laevis* count was not associated with variation in plasma chloride.

Our initial glucose model revealed no significant interaction between *P. laevis* count and treatment group ($p = 0.391$). Removal of the *P. laevis* count by treatment group interaction term lowered the model AIC value by ~ 12.1. No significant association was found between blood glucose and *P. laevis* count in this model (Table 5; Fig. 4). Glucose levels in the 24SW and 72SW groups were significantly lower than in the 24FW group (Table 3; Table 5). This model also revealed that blood glucose was significantly negatively related to Fulton's K (Table 5).

Our initial cortisol model revealed no significant interaction between *P. laevis* count and treatment group ($p = 0.571$). Removal of the *P. laevis* count by treatment group interaction terms lowered the model AIC value by ~ 16.1. The main effect of *P. laevis* count was not significant in the model without this interaction (Table 6; Fig. 4). This model revealed a significant increase in plasma cortisol in the 24SW treatment group relative to the 24FW treatment group and a non-significant increase in cortisol in the 72SW relative to 24FW group (Table 3; Table 6).

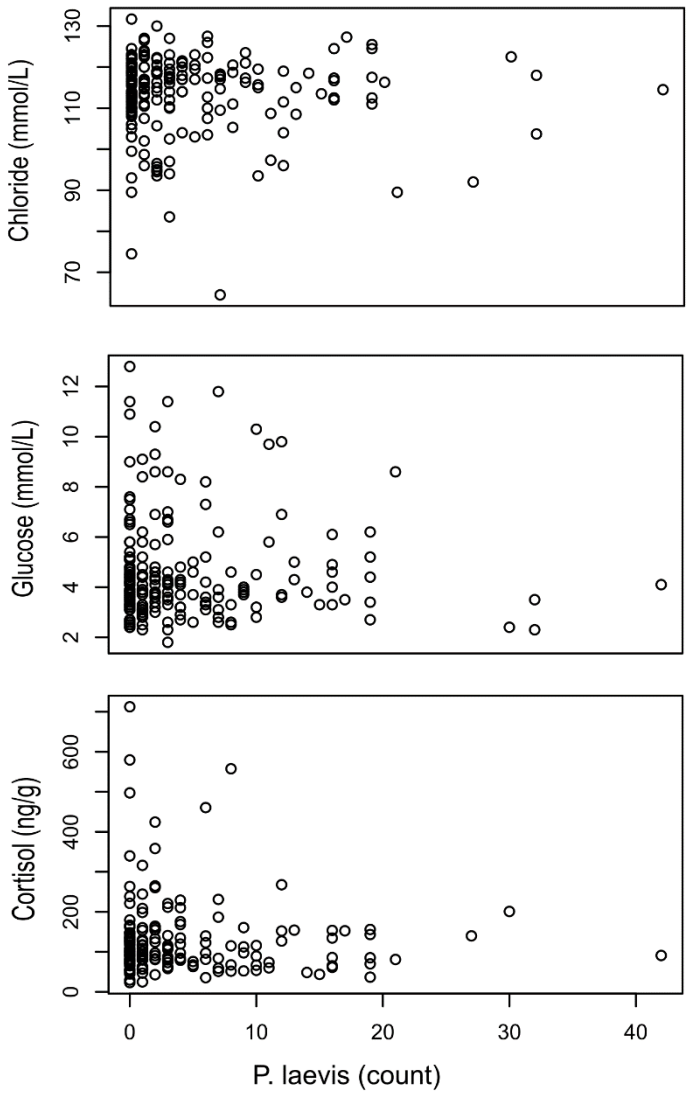


Figure 4. Plasma chloride concentration (mmo/l) vs *P. laevis* count, blood glucose concentration (mmol/l) vs *P. laevis* count and plasma cortisol concentration (mmol/l) vs *P. laevis* count for all smolts used in the experiment (n = 198).

Table 3. Mean and standard deviations for each blood parameter and physical measurements for each treatment group

Treatment Group	24FW	24SW	72SW
Chloride	103.9 ± 10.1	117.7 ± 3.9	119.3 ± 4.8
Cortisol	96.9 ± 58.6	151.0 ± 110.7	133.9 ± 107.7
Glucose	6.6 ± 2.6	4.0 ± 0.9	3.3 ± 0.7
Fork length (mm)	139.9 ± 9.1	138.1 ± 7.9	138.7 ± 8.5
Weight (g)	24.5 ± 5.1	22.8 ± 4.1	23.1 ± 4.7
Condition factor (K)	0.884 ± 0.063	0.858 ± 0.054	0.855 ± 0.058

Table 4. Parameter estimates from the linear model where chloride was the response variable. Intercept corresponds to females in treatment group 24FW in Tank 1 sampled by Operator A.

	Value	Std. Error	t-value	p-value
(Intercept)	116.899	6.076	19.241	<0.001
P. laevis	-0.060	0.053	-1.123	0.263
Treatment Group: 24SW	13.363	1.384	9.655	<0.001
Treatment Group: 72SW	14.998	1.389	10.796	<0.001
Fulton's K	-13.864	6.704	-2.068	0.040
Tank 2	-0.238	1.038	-0.229	0.819
Tank 3	-0.195	1.054	-0.185	0.854
Tank 4	-0.218	1.055	-0.207	0.836
Sex: Male	-0.198	0.773	-0.256	0.798
Operator: B	-0.354	0.730	-0.485	0.628

Table 5. Parameter estimates from the linear model where glucose was the response variable. Intercept corresponds to females in treatment group 24FW in Tank 1 sampled by Operator A.

	Value	Std. Error	t-value	p-value
(Intercept)	10.152	1.131	8.978	<0.001
P. laevis	0.013	0.009	1.422	0.157
Treatment Group: 24SW	-2.686	0.313	-8.575	<0.001
Treatment Group: 72SW	-3.481	0.316	-11.028	<0.001
Fulton's K	-3.743	1.224	-3.059	0.003
Tank 2	-0.193	0.183	-1.052	0.294
Tank 3	-0.134	0.186	-0.718	0.474
Tank 4	-0.167	0.193	-0.865	0.388
Sex: Male	-0.199	0.138	-1.439	0.152
Operator: B	-0.196	0.130	-1.509	0.133

Table 6. Parameter estimates from the linear model where (the natural logarithm of) cortisol was the response variable. Intercept corresponds to females in treatment group 24FW in Tank 1 sampled by operator A.

	Value	Std. Error	t-value	p-value
(Intercept)	4.871	0.673	7.237	<0.001
P. laevis	-0.003	0.006	-0.551	0.583
Treatment Group: 24SW	0.353	0.110	3.197	0.002
Treatment Group: 72SW	0.165	0.111	1.484	0.140
Fulton's K	-0.264	0.729	-0.363	0.717
Tank: 2	-0.186	0.149	-1.251	0.213
Tank: 3	-0.175	0.132	-1.322	0.188
Tank: 4	-0.250	0.145	-1.723	0.087
Sex: Male	-0.017	0.086	-0.201	0.841
Operator: B	0.074	0.083	0.889	0.375

Discussion

We found little evidence that natural infection by *Pomphorhynchus laevis* affected the osmoregulatory performance or stress levels of Atlantic salmon smolts immediately prior to, or within the first 72 h of, entry into salt water. Infection prevalence amongst experimental fish was 66.2% and the distribution of infection intensities exhibited greater-than-Poisson variance (raw variance 10.3 times greater than raw mean), with few individuals having very high intensities and many individuals having zero parasites: a common finding in parasitology in general (Poulin, 2007). *P. laevis* consistently survived the first 72 h that smolts spent in salt water. However, although salinity in the saltwater tanks (~ 26 PPT) was representative of local coastal waters, it was lower than in the open ocean habitat of the North Atlantic (~35 PPT). This lower salinity may have made the environment in the saltwater tanks more tolerable for *P. laevis* than open ocean environments but was reflective of conditions experienced by these smolts in the wild.

The widespread distribution of *P. laevis* in Ireland, combined with the preference of the Irish strain for salmonid definitive hosts (Hine and Kennedy, 1974; Munro, Reid and Whitfield, 1990; Byrne et al., 2003; Molloy, Holland and Poole, 1993), implies that anadromous Irish salmonids often enter the marine environment while infected with these acanthocephalan parasites. Indeed, we found that infection prevalence amongst salmon smolts that were captured at the tidal limit of the Burrishoole catchment during the 2016, 2017 and 2018 smolt runs exceeded 65% in all years, with mean infection intensities of 9.2, 7.3 and 6.9 respectively. These infection rates are in line with those reported from other Irish catchments where *Salmo salar* and *P. laevis* coexist (Pippy, 1969a), and previous studies of this species have also found

strong overdispersion in parasite abundance per fish (Brown, 1989; Kennedy, 1974, 1996). Some authors have suggested that post-cyclic transmission (i.e. transmission occurring when a definitive host eats another definitive host) causes such acanthocephalan overdispersion patterns in definitive host species (Valtonen and Crompton, 1990; Lassiere and Crompton, 1988; Kennedy, 1999). However, the small body size and therefore presumably pre-piscivorous diet of the sampled smolts (no fish parts were observed in the stomach contents of the 175 smolts dissected at time of capture in 2016 and 2017) makes post-cyclic transmission from other host fish unlikely in this case. Given the extensive habitat heterogeneity within the Burrishoole catchment (ranging from fast-flowing streams to deep lakes) (Whelan et al., 1998), it is perhaps more likely that differing feeding behaviour in areas with differing densities of the intermediate host *Gammarus duebeni* resulted in contrasting infection opportunities amongst these fish.

Infection intensity amongst infected smolts was not associated with significant variation in any measure of fish size (fork length, weight or Fulton's K). Infected males sampled in 2016 contained significantly more parasites per individual than infected females from the same year (12.8 vs 4.9) although no sex bias in infection intensity was evident in 2017 or 2018. While no significant associations were found between infection prevalence and absolute measures of fish size (i.e. fork length and weight), infected fish were actually in better condition (at least as expressed by Fulton's K) than uninfected fish. At first glance this is surprising, given that smolt condition might be expected to be negatively impacted by parasitic infection. However, salmon are known to undergo a rapid increase in length during smoltification that is not matched by an equivalent increase in weight, leading to a reduction in condition factor (Wedemeyer, Saunders and Clarke, 1980). Thus, if

infection by *P. laevis* caused a reduction in growth (i.e. length gain) during the parr-smolt transformation period, it could account for the comparatively high condition factor observed amongst infected individuals relative to uninfected individuals. Alternatively, though, this finding could simply reflect the fact that pre-smolts that feed more actively in the weeks or months preceding their marine migration may attain increased condition relative to less active feeders but also have higher chances of consuming intermediate hosts (i.e. *Gammarus duebeni*) infected with *P. laevis*, given that new infections of salmonids in Irish waters tend to peak in spring (Molloy, Holland and O'Regan, 1995; Fitzgerald and Mulcahy, 1983). Such seasonal patterns of parasite infections in salmonids are often associated with temporal changes in diet (Prati and Henriksen, 2020). Previous research has shown that many species of acanthocephalan parasites cause substantial damage to their hosts' intestines (Kim et al., 2011), reducing growth rates when infection intensities are high and leading to mortality in extreme cases (Mayer, Dailey and Miller, 2003; Latham and Poulin, 2002). However, if many of the *P. laevis* found in the sampled smolts were relatively recent infections, there may have been insufficient time for their presence to cause a discernible effect on growth. As marine survival can be strongly associated with smolt size (Jonsson, Jonsson and Jonsson, 2017; Gregory, Armstrong and Britton, 2018), any parasite-induced impact on growth or condition factor is likely to have fitness consequences.

As has been reported previously (Dezfuli et al., 2002a), we found that *P. laevis* deeply penetrated all layers of their host's intestinal wall with their praesoma (hooked proboscis), and in some cases even penetrated the peritoneum and adjacent muscle wall, passing completely out of the intestines in the process (Fig. 2A). The anchoring method used by *P. laevis* has been shown to destroy intestinal mucosa

(Wanstall, Thomas and Robotham, 1988), eliciting a localized inflammatory response (Wanstall, Robotham and Thomas, 1986; Dezfuli et al., 2008, 2011) and copious mucus secretion (Dezfuli et al., 2016; Harris, 1972). Although there is only limited evidence indicating that salmonids infected with *P. laevis* suffer reduced growth (Wanstall, 1984), it appears that these infections may cause modifications to the physiological functioning of their host's alimentary tract, potentially reducing control of transepithelial ion transport (Dezfuli et al., 2002a). Thus, we expected that negative impacts from *P. laevis* infection might only manifest when the host entered salt water, where effective osmoregulation requires efficient control of transepithelial ion transport by the intestine (Whittamore, 2012).

As anticipated (i.e. Bowers et al., 2000b; Stewart et al., 2016; Urke et al., 2014), plasma chloride concentrations were significantly higher in smolts sampled after 24 and 72 hours in salt water than in smolts sampled after 24 hours in fresh water. However, *P. laevis* count was not associated with variation in chloride levels in any treatment group, indicating that any intestinal damage caused by *P. laevis* was insufficient to cause osmoregulatory failure. The range of plasma chloride concentrations in the freshwater and saltwater treatment groups were similar to those reported from other studies of Atlantic salmon in freshwater and saltwater environments (Oppedal et al., 1999; Wells et al., 2006; Kolarevic et al., 2014). However, no sampled fish displayed highly elevated chloride levels in line with levels that have been recorded in salmon smolts infected with high numbers of salmon lice (*Lepeophtheirus salmonis*), which indicate compromised hypo-osmoregulatory function (Wagner et al., 2003; Grimnes and Jakobsen, 1996).

As with chloride, plasma cortisol was significantly higher in the 24SW than in the 24FW treatment group although there was a less pronounced increase in the 72SW group relative to the 24FW group. Cortisol is considered a pluripotent hormone that can be beneficial at moderately elevated levels but harmful when highly elevated (Nolan, Reilly and Bonga, 1999). Moderate elevation of cortisol in salmonids stimulates chloride cell division which facilitates increased fluid uptake from the posterior intestine and thereby improves hypo-osmotic regulatory capacity (Cornell et al., 1994). Thus, the observed increase in cortisol at 24 h in salt water (relative to the freshwater group) may serve to boost osmoregulatory capacity upon initial entry into a saline environment. The drop in cortisol between the 24 and 72 h saltwater sampling periods indicates that this stress response declined as blood chloride levels stabilised. *P. laevis* count was not associated with significant variation in plasma cortisol in the freshwater or saltwater treatment groups, indicating that the intestinal damage caused by the *P. laevis* infection intensities observed in this study was insufficient to cause a discernible stress response in smolts in hypoosmotic or hyperosmotic environments.

Hyperglycemia (elevated blood glucose) is a secondary stress response in fish that has been widely used as an indicator of parasite-induced stress in smolts (Finstad et al., 2007; Long, Garver and Jones, 2019; Wagner et al., 2003). No association between glucose and *P. laevis* count was detected in any of the treatment groups, supporting our conclusion that, at these infection intensities, *P. laevis* does not appear to significantly affect stress levels in migratory smolts before or immediately after entry into salt water. Glucose levels were lowest in the group sampled after 72-hours in salt water, however, plasma glucose is also affected by the feeding history and metabolic status of the fish (Wells et al., 2006). Given the extended period of

fasting that this group experienced prior to sampling (72 h vs 24 h in the other treatment groups), it is possible that the comparatively low glucose levels found in the 72SW treatment group resulted from increased caloric deficit.

The results of this study are based on the use of four replicate tanks for each treatment group. However, despite having 66 fish in each treatment group (i.e. moderate to large sample sizes), only a small number of fish had high infection intensities (Fig. 1), and this may have reduced our ability to detect subtle parasite-induced changes in the blood parameters that we investigated. Also, all *P. laevis* found in each treatment group were alive and the vast majority were securely anchored to the intestinal wall by their praesomae, with no sign that others had recently detached (i.e. no vacant perforations in the intestinal wall). When *P. laevis* are anchored to the intestinal wall, their praesoma and inflated proboscis bulb appear to form an effective plug, preventing movement of liquid through the surrounding intestinal perforation. The freshwater strain of *P. laevis* that parasitizes juvenile salmon in the Burrishoole catchment is generally absent from adult salmon when they return to the river system for spawning (Deirdre Cotter, pers. obs.). Additionally, Molloy et al. (1993) found that sea trout returning to the catchment had lower infection prevalence and intensity than were found in emigrating trout smolts, indicating that *P. laevis* are lost at sea. Presumably, after some period in the marine environment many of these acanthocephalans detach from their hosts' intestines, leaving intestinal perforations unplugged and thereby potentially facilitating ingress of salt water into the peritoneal cavity. However, as *P. laevis* in the sampled smolts remained alive and attached after 72 h in salt water we were unable to investigate this possible delayed pathology. As suggested by Pippy (1969), it would be useful for future studies to establish the life span of *P. laevis* in Atlantic salmon at sea.

Given that infection of Atlantic salmon by *P. laevis* is generally restricted to Ireland and, to a much lesser extent, England, Scotland and Wales (Pippy, 1969a), and because the Irish and English strains of *P. laevis* are morphologically and genetically distinct from each other (O'Mahony et al., 2004; O'Mahony, Kennedy and Holland, 2004), there may be scope to use these parasites as biological tags to indicate the geographic origin of salmon caught at sea. However, Pippy (1969b) suggested that the scarcity of *P. laevis* in adult Atlantic salmon caught around Greenland precludes its use in differentiating stocks caught in that area.

The shift from freshwater to marine environments that defines anadromous fishes is inherently stressful, demanding complex physiological responses from migrants that are simultaneously exposed to unfamiliar predators, parasites and pathogens. Mortality rates during this transitional period can be particularly high, and any pre-existing factor that increases stress or interferes with physiological processes such as osmoregulation may compromise long-term survival at sea (Hostetter et al., 2012, 2011; Finstad et al., 2012, 2007). While the contribution of non-lethal stressors to delayed marine mortality is often difficult to detect, particularly in cases where multiple stressors have a cumulative effect, their impacts are likely to play an important role in determining the performance of anadromous populations. We have shown that a high proportion of wild Atlantic salmon smolts entering the marine environment from the Burrishoole catchment in recent years are infected with *P. laevis* and, based on the literature, it appears likely that similar infection rates of smolts are common in Ireland but not elsewhere. However, we found no evidence to indicate that the infection intensities observed amongst the sampled smolts were associated with altered osmoregulatory performance or stress levels in freshwater or saltwater environments. Despite this, it is possible that infection by *P. laevis* causes

pathologies that we did not test for or that occur later in the marine environment.

Given the high prevalence of *P. laevis* infection amongst anadromous salmonid populations in Ireland, it would be valuable to investigate whether such delayed parasite-induced pathologies occur at sea.

References

Bakke, T.A. and Harris, P.D., 1998. Diseases and parasites in wild Atlantic salmon (Salmo salar) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(1), pp.247–266.

Bisbal, G.A. and Specker, J.L., 1991. Cortisol stimulates hypo-osmoregulatory ability in Atlantic salmon, Salmo salar L. *Journal of Fish Biology*, 39(3), pp.421–432.

Bowers, J.M., Mustafa, A., Speare, D.J., Conboy, G.A., Brimacombe, M., Sims, D.E. and Burka, J.F., 2000. The physiological response of Atlantic salmon, Salmo salar L., to a single experimental challenge with sea lice, Lepeophtheirus salmonis. *Journal of Fish Diseases*, 23(3), pp.165–172.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M. and Bolker, B.M., 2017. {glmmTMB} Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, 9(2), pp.378–400.

Brown, A.F., 1989. Seasonal dynamics of the acanthocephalan Pomphorhynchus laevis (Muller , 1776) in its intermediate and preferred definitive hosts. *Journal of Fish Biology*, 34, pp.183–194.

Byrne, C.J., Holland, C. V, Kennedy, C.R. and Poole, W.R., 2003. Interspecific interactions between Acanthocephala in the intestine of brown trout: are they more frequent in Ireland? *Parasitology*, 127, pp.399–409.

Cornell, S.C., Portesi, D.M., Veillette, P.A., Sundell, K. and Specker, J.L., 1994. Cortisol stimulates intestinal fluid uptake in Atlantic salmon (Salmo salar) in the

post-smolt stage. *Fish Physiology and Biochemistry*, 13(3), pp.183–190.

Dawson, L.H.J., Pike, A.W., Houlihan, D.F. and McVicar, A.H., 1998. Effects of salmon lice Lepeophtheirus salmonis on sea trout Salmo trutta at different times after seawater transfer. *Diseases of Aquatic Organisms*, 33, pp.179–186.

Dezfuli, B.S., Bosi, G., DePasquale, J.A., Manera, M. and Giari, L., 2016. Fish innate immunity against intestinal helminths. *Fish and Shellfish Immunology*, 50, pp.274–287.

Dezfuli, B.S., Castaldelli, G., Bo, T., Lorenzoni, M. and Giari, L., 2011. Intestinal immune response of Silurus glanis and Barbus barbus naturally infected with Pomphorhynchus laevis (Acanthocephala). *Parasite Immunology*, 33, pp.116–123.

Dezfuli, B.S., Giari, L., Simoni, E., Bosi, G. and Manera, M., 2002a. Histopathology, immunohistochemistry and ultrastructure of the intestine of Leuciscus cephalus (L.) naturally infected with Pomphorhynchus laevis (Acanthocephala). *Journal of Fish Diseases*, 25, pp.7–14.

Dezfuli, B.S., Lui, A., Boldrini, P., Pironi, F. and Giari, L., 2008. The inflammatory response of fish to helminth parasites. *Parasite*, 15(3), pp.426–433.

Dezfuli, B.S., Pironi, F., Giari, L., Domeneghini, C. and Bosi, G., 2002b. Effect of Pomphorhynchus laevis (Acanthocephala) on putative neuromodulators in the intestine of naturally infected Salmo trutta. *Diseases of Aquatic Organisms*, 51, pp.27–35.

Eames, S.C., Philipson, L.H., Prince, V.E. and Kinkel, M.D., 2010. Blood Sugar Measurement in Zebrafish Reveals Dynamics of Glucose Homeostasis. *Zebrafish*, 7(2), pp.205–213.

Finlay, R., Poole, R., Coughlan, J., Phillips, K.P., Prodöhl, P., Cotter, D., Mcginnity, P. and Reed, T.E., 2020. Telemetry and genetics reveal asymmetric dispersal of a lake-feeding salmonid between inflow and outflow spawning streams at a microgeographic scale. *Ecology and Evolution*, 10(4), pp.1762–1783.

Finstad, B., Kroglund, F., Bjørn, P.A., Nilsen, R., Pettersen, K., Rosseland, B.O., Teien, H., Nilsen, T.O., Stefansson, S.O., Salbu, B., Fiske, P. and Ebbesson, L.O.E., 2012. Salmon lice-induced mortality of Atlantic salmon postsmolts experiencing episodic acidification and recovery in freshwater. *Aquaculture*, 362–363, pp.193–199.

Finstad, B., Kroglund, F., Strand, R., Stefansson, S.O., Bjørn, P.A., Rosseland, B.O., Nilsen, T.O. and Salbu, B., 2007. Salmon lice or suboptimal water quality — Reasons for reduced postsmolt survival? *Aquaculture*, 273, pp.374–383.

Fitzgerald, R.D. and Mulcahy, M.F., 1983. Parasites of salmon Salmo salar L. and trout Salmo trutta L. in the River Shournagh. In: C. Moriarty, ed. *Irish Fisheries Investigations: Advances in Fish Biology in Ireland*. Dublin: The National Committee for Biology of the Royal Irish Academy. pp.24–31.

Genz, J., Esbaugh, A.J. and Grosell, M., 2011. Intestinal transport following transfer to increased salinity in an anadromous fish (Oncorhynchus mykiss). *Comparative Biochemistry and Physiology*, 159(2), pp.150–158.

Gregory, S.D., Armstrong, J.D. and Britton, J.R., 2018. Is bigger really better? Towards improved models for testing how Atlantic salmon Salmo salar smolt size affects marine survival. *Journal of Fish Biology*, 92(3), pp.579–592.

Grimnes, A. and Jakobsen, P.J., 1996. The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. *Journal of Fish Biology*, 49, pp.1179–

1194.

Grosell, M., 2007. Intestinal Transport Processes in Marine Fish Osmoregulation. In: B. Baldisserotto, ed. *Fish Osmoregulation*, 1st ed. Boca Raton: CRC Press.pp.333–357.

Guillen-Hernandez, S. and Whitfield, P.J., 2001. A comparison of freshwater and marine/ estuarine strains of Pomphorhynchus laevis occurring sympatrically in flounder, Platichthys flesus, in the tidal Thames. *Journal of Helminthology*, 75, pp.237–243.

Handeland, S.O., Imsland, A.K., Nilsen, T.O., Ebbesson, L.O.E., Hosfeld, C.D., Pedrosa, C., Toften, H. and Stefansson, S.O., 2014. Osmoregulation in Atlantic salmon Salmo salar smolts transferred to seawater at different temperatures. *Journal of Fish Biology*, 85(4), pp.1163–1176.

Harris, J.E., 1972. The Immune Response of a Cyprinid Fish to the Acanthocephalan Pomphorhynchys Laevis. *International Journal for Parasitology*, 2, pp.459–469.

Hartig, F., 2019. *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)*.

Hine, P.M. and Kennedy, C.R., 1974. Observations on the distribution, specificity and pathogenicity of the acanthocephalan Pomphorhynchus laevis (Muller). *Journal of Fish Biology*, 6, pp.521–535.

Hohenadler, M.A.A., Nachev, M., Thielen, F., Taraschewski, H., Grabner, D. and Sures, B., 2018. Pomphorhynchus laevis: An invasive species in the river Rhine? *Biological Invasions*, 20, pp.207–217.

Hostetter, N.J., Evans, A.F., Roby, D.D. and Collis, K., 2012. Susceptibility of

Juvenile Steelhead to Avian Predation : the Influence of Individual Fish Characteristics and River Conditions Susceptibility of Juvenile Steelhead to Avian Predation : the Influence of Individual Fish Characteristics and River Conditions. *Transactions ofthe American Fisheries Society*, 141, pp.1586–1599.

Hostetter, N.J., Evans, A.F., Roby, D.D., Collis, K., Hawbecker, M., Sandford, B.P., Thompson, D.E. and Loge, F.J., 2011. Relationship of external fish condition to pathogen prevalence and out-migration survival in juvenile steelhead. *Transactions of the American Fisheries Society*, 140(5), pp.1158–1171.

Hvas, M., Karlsbakk, E., Mæhle, S., Wright, D.W. and Oppedal, F., 2017. The gill parasite Paramoeba perurans compromises aerobic scope, swimming capacity and ion balance in Atlantic salmon. *Conservation Physiology*, 5, pp.1–12.

Iversen, M., Finstad, B. and Nilssen, K.J., 1998. Recovery from loading and transport stress in Atlantic salmon (Salmo salar L.) smolts. *Aquaculture*, 168(1–4), pp.387–394.

J, P., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S. and Van Willigen, B., 2019. *nlme: Linear and Nonlinear Mixed Effects Models*.

Jonsson, B., Jonsson, M. and Jonsson, N., 2017. Influences of migration phenology on survival are size dependent in juvenile Atlantic salmon. *Canadian Journal of Zoology*, 95(8), pp.581–587.

Kennedy, C.R., 1974. The importance of parasite mortality in regulating the population size of the Acanthocephalan Pomphorhynchus laevis in goldfish. *Parasitology*, 68, pp.93–101.

Kennedy, C.R., 1996. Colonization and establishment of Pomphorhynchus laevis

(Acanthocephala) in an isolated English river. *Journal of Helminthology (1996)*, 70, pp.27–31.

Kennedy, C.R., 1999. Post-cyclic transmission in Pomphorhynchus laevis (Acanthocephala). *Folia Parasitologica*, 46, pp.111–116.

Kennedy, C.R., Bates, R.M. and Brown, A.F., 1989. Discontinuous distributions of the fish acanthocephalans Pomphorhynchus laevis and Acanthocephalus anguillae in Britain and Ireland : an hypothesis. *Journal of Fish Biology*, 34, pp.607–619.

Kim, S.R., Lee, J.S., Kim, J.H., Oh, M.J., Kim, C.S., Park, M.A. and Park, J.J., 2011. Fine structure of Longicollum pagrosomi (Acanthocephala: Pomphorhynchidae) and intestinal histopathology of the red sea bream, Pagrus major, infected with acanthocephalans. *Parasitology Research*, 109(1), pp.175–184.

Kolarevic, J., Baeverfjord, G., Takle, H., Ytteborg, E., Reiten, B.K.M., Nergård, S. and Terjesen, B.F., 2014. Performance and welfare of Atlantic salmon smolt reared in recirculating or flow through aquaculture systems. *Aquaculture*, 432, pp.15–25.

Krkošek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B. and Todd, C.D., 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. *Proceedings of the Royal Society B: Biological Sciences*, 280, pp.1–8.

Lassiere, O.L. and Crompton, D.W.T., 1988. Evidence for post-cyclic transmission in the life-history of Neoechinorhynchus rutili (Acanthocephala). *Parasitology*, 97, pp.339–343.

Latham, A.D.M. and Poulin, R., 2002. Field evidence of the impact of two acanthocephalan parasites on the mortality of three species of New Zealand shore crabs (Brachyura). *Marine Biology*, 141(6), pp.1131–1139.

Long, A., Garver, K.A. and Jones, S.R.M., 2019. Differential Effects of Adult Salmon Lice Lepeophtheirus salmonis on Physiological Responses of Sockeye Salmon and Atlantic Salmon. *Journal ofAquatic Animal Health*, 31, pp.75–87.

Martinez-Porchas, M., Martinez-Cordova, L.T. and Ramos-Enriquez, R., 2009. Cortisol and Glucose : Reliable indicators of fish stress ? *Journal of Aquatic Sciences*, 4, pp.158–178.

Mayer, K.A., Dailey, M.D. and Miller, M.A., 2003. Helminth parasites of the southern sea otter Enhydra lutris nereis in central California: Abundance, distribution and pathology. *Diseases of Aquatic Organisms*, 53(1), pp.77–88.

McCormick, S.D., 2012. Smolt Physiology and Endocrinology. *Euryhaline Fishes: Fish Physiology*, 32, pp.199–251.

Molloy, S., Holland, C. and O'Regan, M., 1995. Population biology of Pomphorhynchus laevis in brown trout from two lakes in the west of Ireland. *Journal of Helminthology*, 69, pp.229–235.

Molloy, S., Holland, C. and Poole, R., 1993. Helminth parasites of brown and sea trout Salmo trutta L. from the west coast of Ireland. *Proceedings of the Royal Irish Academy - Section B Biology and Environment*, 93B(3), pp.137–142.

Munro, M.A., Reid, A. and Whitfield, P.J., 1990. Genomic divergence in the ecologically differentiated English freshwater and marine strains of Pomphorhynchus laevis (Acanthocephala: Palaeacanthocephala): a preliminary investigation. *Parasitology*, 101, pp.451–454.

Munro, M.A., Whitfield, P.J. and Diffley, R., 1989. Pomphorhynchus laevis (Muller) in the flounder , Platichthys flesus L ., in the tidal River Thames: population

structure, microhabitat utilization and reproductive status in the field and under conditions of controlled salinity. *Journal of Fish Biology*, 35, pp.719–735.

Nolan, D.T., Reilly, P. and Bonga, S.E.W., 1999. Infection with low numbers of the sea louse Lepeophtheirus salmonis induces stress-related effects in postsmolt Atlantic salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, 56, pp.947–959.

O'Mahony, E.M., Bradley, D.G., Kennedy, C.R. and Holland, C. V, 2004. Evidence for the hypothesis of strain formation in Pomphorhynchus laevis (Acanthocephala) : an investigation using mitochondrial DNA sequences. *Parasitology*, 129, pp.341–347.

O'Mahony, E.M.O., Kennedy, C.R. and Holland, C. V, 2004. Comparison of morphological characters in Irish and English populations of the acanthocephalan Pomphorhynchus laevis (Müller, 1776). (59), pp.147–157.

Oppedal, F., Taranger, G.L., Juell, J.-E. and Hansen, T., 1999. Growth, osmoregulation and sexual maturation of underyearling Atlantic salmon smolt Salmo salar L. exposed to different intensities of continuous light in sea cages. *Aquaculture Research*, 30, pp.491–499.

Perrot-Minnot, M.J., Bollache, L. and Lagrue, C., 2020. Distribution of Pomphorhynchus laevis s.l. (Acanthocephala) among fish species at a local scale: importance of fish biomass density. *Journal of Helminthology*, 94, pp.1–10.

Pippy, J., 1969a. Pomphorhynchus laevis (Zoega) Müller, 1776 (Acanthocephala) in Atlantic Salmon (Salmo salar) and Its Use as a Biological Tag. *Journal of the Fisheries Research Board of Canada*, 26(4), pp.909–919.

Pippy, J.H.C., 1969b. Preliminary report on parasites as biological tags in Atlantic salmon (Salmo salar). I. Investigations 1966 to 1968. *Canadian Journal of Fisheries and Aquatic Sciences*, 134, p.44.

Poole, W.R., Dillane, M., Deeyto, E., Rogan, G., Mcginnity, P. and Whelan, K., 2007. Characteristics of the Burrishoole Sea Trout Population: Census, Marine Survival, Enhancement and Stock-Recruitment Relationship, 1971-2003. In: G. Harris and N. Milner, eds. *Sea Trout: Biology, Conservation and Management*. Wiley-Blackwell.pp.279–306.

Poole, W.R., Nolan, D. and Tully, O., 2000. Modelling the effects of capture and sea lice [Lepeophtheirus salmonis (Kroyer)] infestation on the cortisol stress response in trout. *Aquaculture Research*, 31(11), pp.835–841.

Poulin, R., 2007. Are there general laws in parasite ecology? *Parasitology*, 134(6), pp.763–776.

Prati, S. and Henriksen, E.H., 2020. Seasonal dietary shifts enhance parasite transmission to lake salmonids during ice cover. *Ecology and Evolution*, pp.1–13.

R_Core_Team, 2019. *R: A Language and Environment for Statistical Computing*.

Redding, J.M. and Schreck, C.B., 1983. Influence of Ambient Salinity on Osmoregulation and Cortisol Concentration in Yearling Coho Salmon during Stress. *Transactions of the American Fisheries Society*, 112(6), pp.800–807.

Ricker, W.E., 1975. *Computation and interpretation of biological statistics of fish populations. Journal of the Fisheries Research Board of Canada*, Ottawa.

Roohi, J.D., Pazooki, J. and Sattari, M., 2015. The first record of Pomphorhynchus laevis (Acanthocephala) in Chub, Squalius cephalus (Linnaeus, 1758) from

Gamasiab River, Hamedan, Iran. *Caspian Journal of Environmental Science*, 13(2), pp.173–178.

Shephard, S. and Gargan, P., 2017. Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. *Aquaculture Environment Interactions*, 9, pp.181–192.

Stefansson, S.O., Haugland, M., Björnsson, B.T., McCormick, S.D., Holm, M., Ebbesson, L.O.E., Holst, J.C. and Nilsen, T.O., 2012. Growth, osmoregulation and endocrine changes in wild Atlantic salmon smolts and post-smolts during marine migration. *Aquaculture*, 362–363, pp.127–136.

Stewart, H.A., Noakes, D.L.G., Cogliati, K.M., Peterson, J.T., Iversen, M.H. and Schreck, C.B., 2016. Salinity effects on plasma ion levels, cortisol, and osmolality in Chinook salmon following lethal sampling. *Comparative Biochemistry and Physiology -Part A*, 192, pp.38–43.

Strand, R. and Finstad, B., 2007. Migratory behaviour in relation to smolt development and releasing strategies in Atlantic salmon (Salmo salar L.) smolts. *Aquaculture*, 273(2–3), pp.277–283.

Thorstad, E.B., Todd, C.D., Uglem, I., Bjørn, P.A., Gargan, P.G., Vollset, K.W., Halttunen, E., Kålås, S., Berg, M. and Finstad, B., 2015. Effects of salmon lice Lepeophtheirus salmonis on wild sea trout salmo trutta - A literature review. *Aquaculture Environment Interactions*, 7(2), pp.91–113.

Urke, H.A., Arnekleiv, J. V., Nilsen, T.O. and Nilssen, K.J., 2014. Development of seawater tolerance and subsequent downstream migration in wild and stocked young-of-the-year derived Atlantic salmon Salmo salar smolts. *Journal of Fish Biology*, 84(1), pp.178–192.

Valtonen, E.T. and Crompton, D.W.T., 1990. Acanthocephala in fish from the Bothnian Bay, Finland. *Journal of Zoology*, 220, pp.619–639.

Wagner, G.N., McKinley, R.S., Bjørn, P.A. and Finstad, B., 2003. Physiological impact of sea lice on swimming performance of Atlantic salmon. *Journal of Fish Biology*, 62(5), pp.1000–1009.

Wanstall, S.T., 1984. *A study of the pathobiology of Pomphorhynchus laevis Muller in freshwater fish*. Derbyshire College of Further Education.

Wanstall, S.T., Robotham, P.W.J. and Thomas, J.S., 1986. Pathological changes induced by Pomphorbynchus laevis Muller (Acanthocephala) in the gut of rainbow trout, Salmo gairdneri Richardson. *Parasitenkunde*, 72, pp.105–114.

Wanstall, S.T., Thomas, J.S. and Robotham, P.W.J., 1988. The pathology caused by Pomphorhynchus laevis Muller in the alimentary tract of the stone loach, Noemacheilus harbatulus (L.). *Journal of Fish Diseases*, 11, pp.511–523.

Wedemeyer, G.A., Saunders, R.L. and Clarke, W.C., 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. *Marine Fisheries Review*, 4(6), pp.1–14.

Wells, A., Grierson, C.E., MacKenzie, M., Russon, I.J., Reinardy, H., Middlemiss, C., Bjørn, P.A., Finstad, B., Bonga, S.E.W., Todd, C.D. and Hazon, N., 2006. Physiological effects of simultaneous, abrupt seawater entry and sea lice (Lepeophtheirus salmonis) infestation of wild, sea-run brown trout (Salmo trutta) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(12), pp.2809–2821.

Whelan, K.F., Poole, W.R., McGinnity, P., Rogan, G. and Cotter, D., 1998. The Burrishoole System. In: *Studies of Irish Rivers and Lakes, Essays on the occasion of*

the XXVII Congress of Societas Internationalis Limnologiae (SIL). Dublin.pp.191–212.

Whittamore, J.M., 2012. Osmoregulation and epithelial water transport: Lessons from the intestine of marine teleost fish. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 182(1), pp.1–39.

Ziolkowska, M., Chibani, M., Kijewska, M. and Rokicki, J., 2000. The occurrence of Pomphorhynchus laevis (Muller, 1776) (Acanthocephala) and the age of the flounder (Platichthys flesus , L.). *Helminthology*, 37(3), pp.159–161.

Chapter 3

Development of a double-breakaway pass-through PIT-tag antenna system for flood-prone rivers

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Author Contributions: RF designed, built, installed and maintained the antenna. RF wrote the first draft of the manuscript. All authors contributed revision of the manuscript and gave final approval for publication.

Abstract

Pass-through passive integrated transponder (PIT) antennae are often used in river and stream habitats to monitor the movement of aquatic species. Where these habitats are prone to high flows containing suspended debris, traditional pass-through antenna designs are particularly vulnerable to damage which can be time consuming and expensive to repair and lead to extended gaps in data collection. We designed and tested a novel pass-through half duplex (HDX) antenna system that allows the antenna loop to (1) break away from one river bank under predetermined strain and (2) split into two separate cables, thereby shedding entangled debris that could otherwise damage or dislodge the antenna system. After break away events, our system can be rapidly reconnected and redeployed without the need for personnel to enter the water, reducing maintenance time and costs while minimizing gaps in data. In locations where pass-through antennae are prone to flood damage, this system offers distinct advantages over traditional designs.

Introduction

Due to their small size, low cost and lack of internal batteries, PIT tags have proven to be a valuable tool for studying freshwater fish at various stages of their life histories (Haraldstad et al., 2016; Furey et al., 2016; Winter et al., 2016; Conallin et al., 2012; Bond et al., 2007; Castro-Santos, Haro and Walk, 1996; Dodd, Cowx and Bolland, 2018). Stationary in-stream antennae are commonly used to monitor the movement of PIT-tagged fish in dynamic fluvial environments where antennae are prone to damage from high flows and debris (Cooke et al., 2013). A number of flat-bed/pass-by antenna designs (i.e. where the antenna lies flat on the streambed) have

been developed that are relatively robust to damage from flotsam (Johnston, Berube and Bergeron, 2009; Nunnallee et al., 1998; Greenberg and Giller, 2000; Lucas et al., 1999; Kazyak and Zydlewski, 2012; Armstrong, Braithwaite and Rycroft, 1996). While flat-bed antennae are effective at detecting tags passing close to the streambed, their horizontal orientation limits their vertical read range. Pass-through antennae, by virtue of their vertical orientation, are able to detect tags that are significantly higher in the water column. Additionally, because PIT tags generally lie horizontally when implanted in fish, they are ideally oriented for detection by pass-through antennae. These attributes make pass-through antennae particularly well suited to sites with relatively deep water or to studies where the morphology of the target species necessitates the use of small (i.e. 12 mm) PIT tags that produce weak signals. However, the vertical orientation of pass-through antennae can expose them to greater stresses than flat-bed designs, particularly in cases where flotsam becomes caught on the antenna loop.

In order to investigate the migratory phenology and survival of Atlantic salmon *Salmo salar* L. and brown trout *Salmo trutta* L. smolts, we constructed and installed a series of five HDX PIT antennae (ranging in width from 2.5 m to 18 m) in the Burrishoole river system in the West of Ireland (Fig. 1). HDX systems were chosen over FDX systems due to their ability to power wide, flexible antennae that are simple to construct and present a reduced profile in the water column. Due to water depth at our installation sites, the tendency of smolts to travel close to the water surface (Moore et al., 1998; Thorstad et al., 2012; Scruton et al., 2005) and our fish size-necessitated use of 12 mm tags, pass-through antennae were deemed preferable to flat-beds. However, the Burrishoole river system is prone to frequent high flow events that often carry large debris from forestry located upstream (O'Toole et al.,

2015 and Fig. 2). Initial installations for this project that were based on traditional pass-through designs proved susceptible to catastrophic damage during floods, particularly when large flotsam became entangled in the loop of the antenna cable. Such occurrences necessitated the construction and installation of replacement antenna systems, leading to extended gaps in data collection and representing significant costs in materials and labour. In response, we designed a new pass-through antenna system with the requirements that (a) high flow events or floating debris would not cause significant damage, and (b) any post-flood maintenance or redeployment of the system should be simple, rapid and cheap.

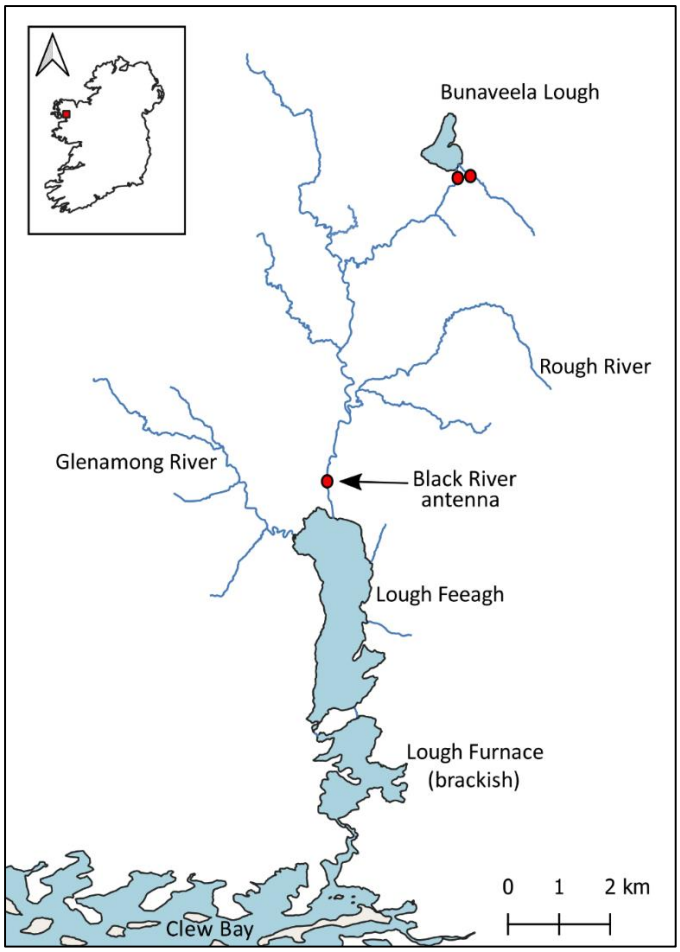


Figure 1. —Map of the Burrishoole catchment with antenna locations marked as red circles. Each of the two northerly locations represent antenna arrays comprised of two antennae.



Figure 2. — Black river antenna location at normal river height (A) and during a flood (B). The top of the antenna is visible just above the water surface in image (A).

Materials and methods

Here we describe an antenna system installed in March 2018 at our most challenging site (stream width and height 1800 cm and ~ 65 cm respectively under normal flow conditions). To span this section of river, we constructed a 1750 cm X 75 cm rectangular antenna from a single turn of 6 mm^2 (~ 9 American wire gauge (AWG) equivalent) multi-strand PVC sheathed coper wire (Fig.3, part 1). Antenna inductance, as measured with an Extrech Instruments LCR meter, was 41.3 μH. The antenna cable was passed through a 12 mm internal diameter braided PVC hose pipe (Fig. 3 and 4, part. 2) to provide protection from abrasion. A 20 cm section of hose located at the intended midpoint of the antenna loop was slit lengthways, cut

crosswise at each end, and removed (Fig. 3, 4 and 5, part 3). The antenna cable was severed at the midpoint of the gap created and male and female pin components from a seven pin trailer board plug were soldered to the severed ends of the cable, allowing these ends to be reconnected (Fig. 5 a).

Once connected, the plug assembly was sealed with electrical tape to provide waterproofing and a minor degree of tensile support. The previously removed section of hose (part 3) was replaced in its original position and secured to the cut ends of the hose with cable ties and stoppers made from electrical tape (Fig. 4 and 5 b), allowing this section of hose and the cable within to separate or break away under relatively low strain. The sections of hose covering the two horizontal (top and bottom) sections of the antenna were cable-tied to two sections of 10 mm pre-stretched dyneema support ropes (Fig. 3 and 4, part 4) with a rated breaking strain of 5000 kg. A MIN-E-MAX™ (DCD Design and Manufacturing Ltd., British Columbia) breakaway connector (Part No. 00530-010) loaded with a 600 lb (272 kg) breakaway pin (Part No. 00555-006) (Fig. 3 and 4, part 5) was attached to each support rope at the end nearest the plug assembly, allowing the rope to break away at this location as strain on it approached 300 kg.

Stainless steel carabiners (1500 kg breaking strain) were used to secure the breakaway connectors to two M10 eye bolts (Fig. 4, part 6) that were driven through pre-drilled holes located 7 cm and 82 cm from the bottom of a 10 cm wide, 200 cm long pressure treated round timber post (Fig. 3 and 4, part 7). Each eye bolt was secured with washers and two lock nuts. A second 10 cm wide round timber post (Fig. 3 and 6, part 8) measuring 270 cm was furnished with eye bolts in the same manner as the first post and single (Fig 3 and 6, part 9) and double (Fig. 3 part 10) blocks (pulleys) with a 1500 kg rating were secured to the bottom and top eye bolt

respectively. The free end of the lower support rope was passed through the bottom block before it and the upper rope were passed through the top block and secured to a hand winch (Fig. 3, part 11) mounted to the top of the support pole (part 8) with M10 bolts, lock nuts and a bracing plate. Two mounting tubes (Fig. 3 and 6, part 12) were constructed by cutting two 8 mm wide strips from opposite sides of two 180 cm long, 15 mm-walled HDPE pipes with 10.5 cm internal diameters, leaving 7 cm of uncut material at one end (the bottom) of each tube.

The antenna support poles were inserted into the mounting tubes (Fig. 6) until the protruding lower eye bolts reached the uncut end. Two 30 mm wide ratchet straps (Fig. 4 and 6, part 13) were used to connect three Duckbill Earth Anchors ® (MacLean Civil Products, South Carolina) (Fig. 3 and 6, part 14) to the rear uncut bottom section of each tube. Two ratchet straps were also used to connect three Duckbill Earth Anchors to the rear of each tube just above the top eye bolt while pressure from these straps also clamped the tubes securely onto the support poles. Extended drive rods were used to secure the lower Duckbill anchors to the streambed at each bank before the upper anchors were secured horizontally into the bank itself. The hand winch was then used to simultaneously tension the top and bottom support ropes after which the handle was removed to discourage tampering.

Once the system was installed as described above, an ATC Auto Tuner (Oregon RFID, Oregon) (Fig. 3, part 15) was mounted to a vertical post located beside support pole (part 8), and connected to the free ends of the antenna cable in order to adjust antenna capacitance. A Multi-Antenna HDX Reader (Oregon RFID, Oregon) was connected to the auto tuner by shielded Belden 9207 twinaxial cable which transmits power and data. Due to danger from flooding (Fig. 2), the reader was located in a sealed box on high ground 60 m from the antenna installation site and

the twinaxial cable was buried to ~ 10 cm. Power for the system was provided by a bank of five 120 Ah AGM 12V batteries connected in parallel which were swapped out periodically.

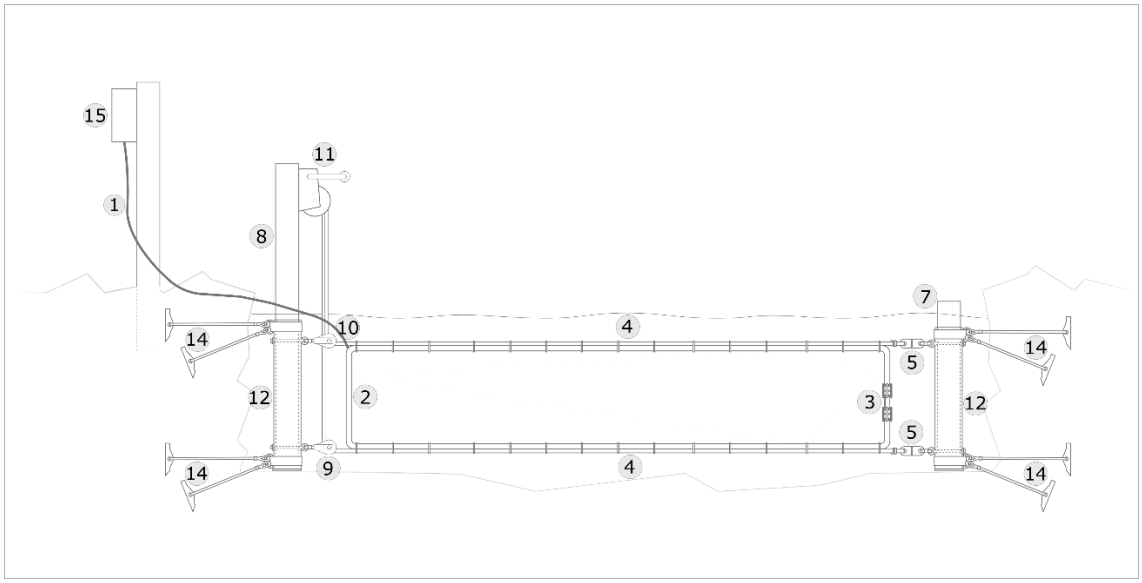


Figure 3. —Diagram of the double breakaway antenna system (not to scale). Numbered circles designate parts described in the Antenna Construction section.

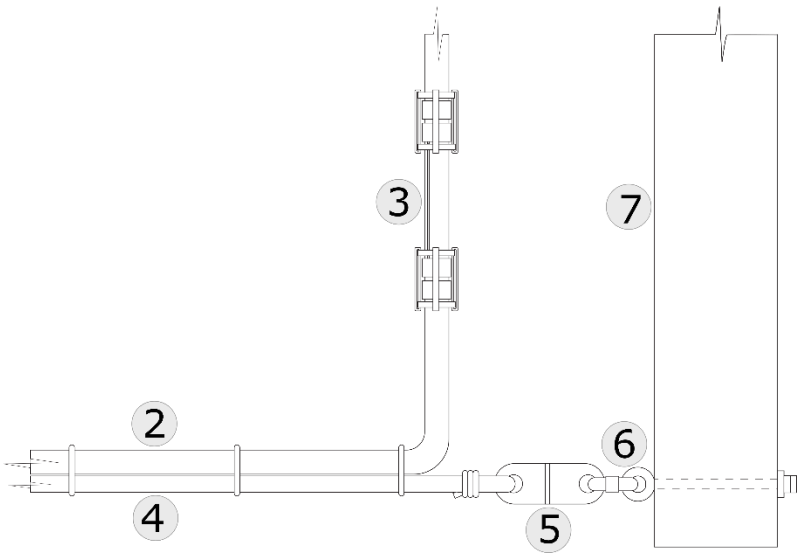


Figure 4. —Diagram showing the lower breakaway connector assembly and the breakaway section of the antenna cable (not to scale). Numbered circles designate parts described in the Antenna Construction section.

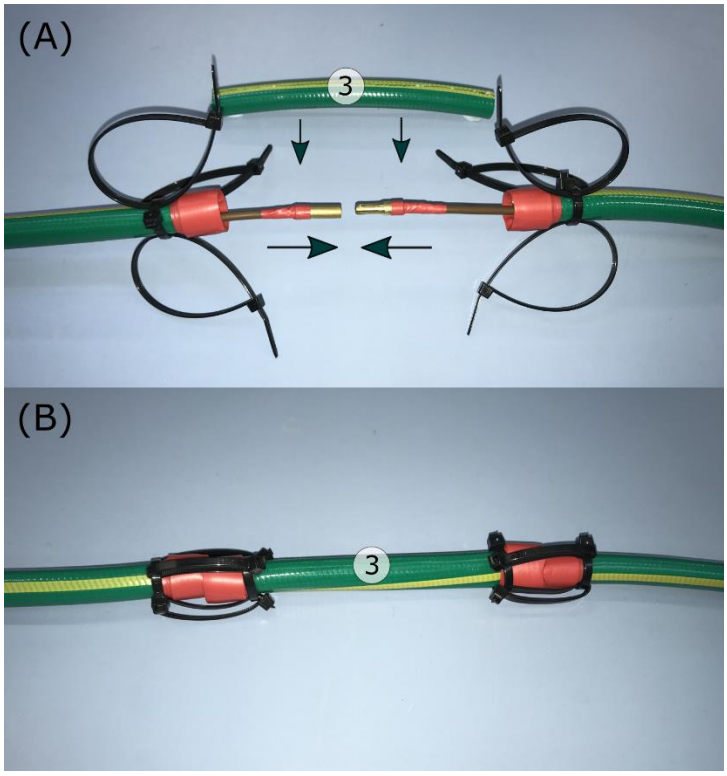
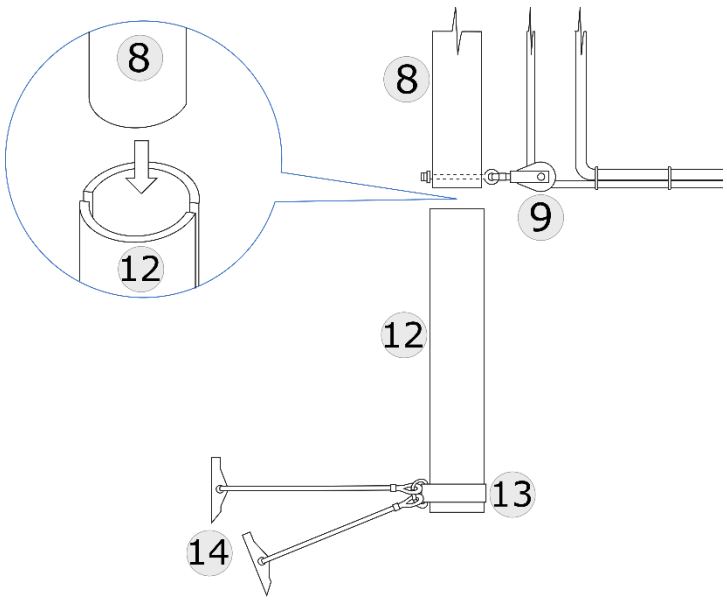


Figure 5. — Photograph of the breakaway plug assembly (A) separated and (B) assembled and ready for deployment.



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Figure 6. —Diagram showing the lower (single) pulley assembly and the method of inserting the support poles into the mounting tubes (not to scale). Numbered circles designate parts described in the Antenna Construction section.

Results

Tag detection

We tested the in-stream performance of our antenna with 12 mm 134.2 kHz HDX tags manufactured by Oregon RFID and Biomark Inc., Idaho. When orientated perpendicular to the antenna, both companies' tags were detected at all points within the loop and up to 10 cm outside it, providing ~ 95 cm of vertical detection coverage and ~ 1770 cm of horizontal coverage. Tags were detected from roughly 20 cm upstream to 20 cm downstream of the antenna, providing a 'reading frame' (*sensu* Bond et al., 2007) of about 40 cm.

Breakaway operation and maintenance

Between March 2018 and September 2019, regular high flow events occurred in the Burrishoole catchment (Fig. 7). On seven of these occasions the strain on the antenna system exceeded the predetermined pin limit (272 kg), causing the MIN-E-MAX™ breakaway connectors to separate. On each occasion the trailer plug pin connection also separated, allowing flotsam to pass without becoming tangled in the antenna cable. Consequently, no significant damage to the antenna system occurred within the operating period. After breakaway events, the loose ends of the antenna were laid on the western river bank (nearest the autotuner) and the trailer plug assembly was reconnected and sealed as described above. The upper ratchet straps were briefly removed from the mounting tube on the opposite bank, allowing the support pole (part 7) to be removed and brought to the western river bank where the upper and lower MIN-E-MAX™ breakaways could be reconnected and loaded with new pins.

The winch was then used to slacken the support ropes, allowing the support pole (part 7) to be dragged across the river with a rope and reinstalled in its mounting tube as described above. In situations where the far bank can only be accessed by wading, it may necessary to carry the support pole across. Finally, the support ropes were re-tensioned with the winch, allowing the antenna to recommence operation. The complete post-breakaway reinstallation process can be accomplished by two operators in less than 45 minutes and, in cases where both banks are accessible without wading, does not require either operator to enter the river. Additionally, if required, the two support poles (part 7 and 8) can be removed from their mounting tubes (part 12) in minutes, allowing the entire antenna to be removed from the installation site and easily reinstalled at a later date. In order to protect the mounting tubes in the interim it is recommended to insert a 10 cm wide round timber post into each (roughly equal in length to the tube) and tighten the upper ratchet straps (part. 13).

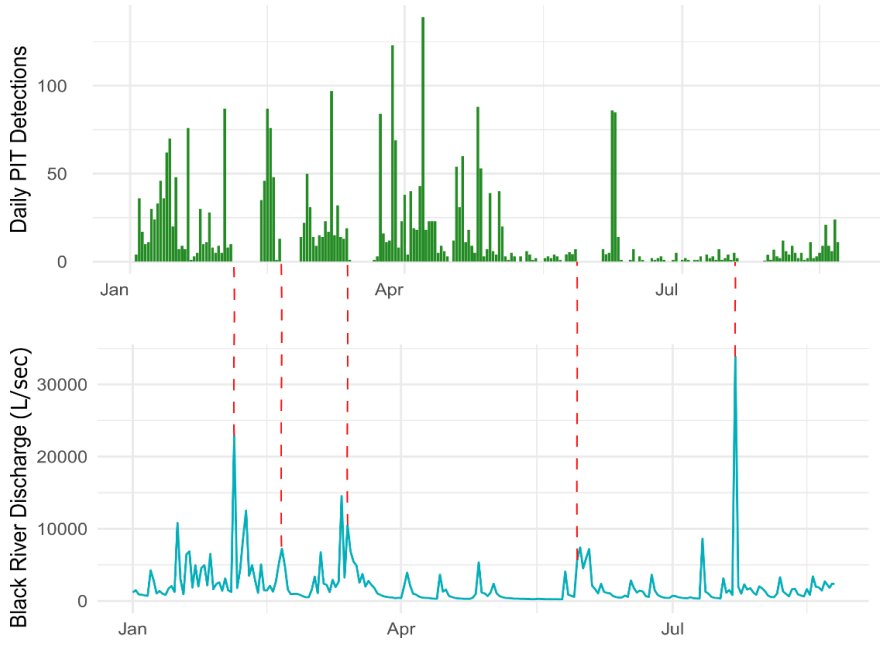


Figure 7. —Number of PIT tag detections recorded on the Black River antenna and average daily discharge (L/sec) from the Black River, January 2019 to August 2019. Antenna breakaway events are indicated by dashed vertical lines.

Discussion

At its most basic, a PIT antenna is an unbroken loop of conductive cable. Pass-through, as opposed to flat-bed, PIT antennae are often used in river and stream habitats to monitor the movement of aquatic species (Bond et al., 2007; Haraldstad et al., 2016; Winter et al., 2016; Zydlewski et al., 2001; Kazyak and Zydlewski, 2012). When installed in a river in pass-through orientation, PIT antennae can be exposed to significant strain that increases dramatically as antenna size or water velocity increases or when debris become entangled in the cable loop. Against this background, our double-breakaway system exhibits a number of major advantages over traditional pass-through designs. Firstly, by breaking away from one bank and then opening the antenna loop, our system can withstand high flow events and the passage of suspended debris without sustaining significant damage. Secondly, after breakaway events occur, the system can be rapidly redeployed by two operators. Furthermore, if both banks of the river or stream are accessible, redeployment can be carried out without the need for personnel to enter the river. Finally, the use of mounting tubes allows the entire antenna to be rapidly removed and reinstalled at a later date, a beneficial feature for monitoring programmes focused on seasonal phenomena (i.e. salmonid smolt or spawning migrations).

The system described here represents a design framework that can and should be modified to suit local conditions. Construction, assembly and installation of the system is relatively simple but does require rudimentary DIY experience as well as a practical understanding of PIT technology. Due to our requirement for ~ 18 m (stream width) of horizontal PIT tag detection coverage at our installation site, a single loop antenna was found to outperform multi-loop designs. Where stream-width is narrower (i.e. < 10 m), multi-loop antennae are often required to achieve

appropriate inductance (Miller, 2011; Arnaud et al., 2015; EE-Web, 2020; Steinke and Anderson, 2011). These can be accommodated by the system described here with the minor modification that each additional turn of cable will require an additional plug assembly. We conservatively used 600 lbs (272 kg) breakaway pins in our system due to the soft river substrate (peat silt) and bank composition at our installation site which reduced the tensile grip of the Duckbill anchors. Where anchors can be mounted more securely, stronger breakaway pins may reduce the frequency of breakaway events and increase continuity of data collection. However, it is crucial to ensure that all load-bearing components used in the antenna system are significantly stronger than the chosen breakaway pins.

River substrate in some areas may prove to be unsuitable for securing Duckbill anchors, particularly in locations where the riverbed is dominated by large rocks. Other mounting equipment may provide a solution in such cases although it may often be preferable to find an alternate location. Additionally, this system can be most easily and securely installed in locations where a river and its banks form a relatively square cross section. Both of these considerations should be taken into account when assessing potential installation sites. As with any PIT antenna installation in fluvial habitats, it is also vital that antenna amperage is maintained within safe limits at all times.

Although pass-through antennae are generally exposed to greater strain than similar-sized flat-beds, their increased vertical read range and detection performance represent distinct advantages as water depth increases. Our double-breakaway system can facilitate the long-term operation of pass-through antennae in locations where high flows and floating debris make traditional pass-through designs unfeasible.

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References

Armstrong, J.D., Braithwaite, V.A. and Rycroft, P., 1996. A flat-bed passive integrated transponder antenna array for monitoring behaviour of Atlantic salmon parr and other fish. *Journal of Fish Biology*, 48, pp.539–541.

Arnaud, F., Piégay, H., Vaudor, L., Bultingaire, L. and Fantino, G., 2015. Technical specifications of low-frequency radio identification bedload tracking from field experiments: Differences in antennas, tags and operators. *Geomorphology*, 238, pp.37–46.

Bond, M.H., Hanson, C. V, Baertsch, R., Hayes, S.A. and MacFarlane, R.B., 2007. A new low-cost instream antenna system for tracking passive integrated transponder (PIT) -tagged fish in small streams. *Transactions of the American Fisheries Society*, 136, pp.562–566.

Castro-Santos, T., Haro, A. and Walk, S., 1996. A passive integrated transponder (PIT) tag system for monitoring fishways. *Fisheries Research*, 28(3), pp.253–261.

Conallin, J., Jyde, M., Filrup, K. and Pedersen, S., 2012. Diel foraging and shelter use of large juvenile brown trout (Salmo trutta) under food satiation. *Knowledge and Management of Aquatic Ecosystems*, 404(5), pp.1–6.

Cooke, S.J., Midwood, J.D., Thiem, J.D., Klimley, P., Lucas, M.C., Thorstad, E.B., Eiler, J., Holbrook, C. and Ebner, B.C., 2013. Tracking animals in freshwater with electronic tags: past, present and future. *Animal Biotelemetry*, 1(5), pp.1–19.

Dodd, J.R., Cowx, I.G. and Bolland, J.D., 2018. Win, win, win: Low cost baffle fish pass provides improved passage efficiency, reduced passage time and broadened passage flows over a low-head weir. *Ecological Engineering*, 120, pp.68–75.

EE-Web, 2020. *Coil Inductance Calculator*. [online] EE-Web. Available at: <https://www.eeweb.com/tools/coil-inductance> [Accessed 19 Apr. 2020].

Furey, N.B., Hinch, S.G., Bass, A.L., Middleton, C.T., Minke-Martin, V. and Lotto, A.G., 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. *Journal of Animal Ecology*, 85, pp.948–959.

Greenberg, L.A. and Giller, P.S., 2000. The potential of flat-bed passive integrated transponder antennae for studying habitat use by stream fishes. *Ecology of Freshwater Fish*, 9, pp.74–80.

Haraldstad, T., Kroglund, F., Kristensen, T., Jonsson, B. and Haugen, T.O., 2016. Diel migration pattern of Atlantic salmon (Salmo salar) and sea trout (Salmo trutta) smolts: an assessment of environmental cues. *Ecology of Freshwater Fish*, 26(4), pp.541–551.

Johnston, P., Berube, F. and Bergeron, N.E., 2009. Development of a flatbed passive integrated transponder antenna grid for continuous monitoring of fishes in natural streams. *Journal of Fish Biology*, 74, pp.1651–1661.

Kazyak, D. and Zydlewski, J., 2012. High-Density Polyethylene Pipe: A New Material for Pass-By Passive Integrated Transponder Antennas. *North American Journal of Fisheries Management*, 32, pp.49–52.

Lucas, M.C., Mercer, T., Armstrong, J.D., McGinty, S. and Rycroft, P., 1999. Use of a Flat-bed passive integrated transponder antenna array to study the migration and behaviour of lowland river fishes at a fish pass. *Fisheries Research*, 44, pp.183–191.

Miller, E.K., 2011. Time-Domain Computation of Loop inductance. *IEEE*, (6),

pp.62–65.

Moore, A., Ives, S., Mead, T.A. and Talks, L., 1998. The migratory behaviour of wild Atlantic salmon (Salmo salar L.) smolts in the River Test and Southampton Water, southern England. *Hydrobiologia*, 371, pp.295–304.

Nunnallee, E.P., Prentice, E.F., Jonasson, B.F. and Patten, W., 1998. Evaluation of a flat-plate PIT tag interrogation system at Bonneville Dam. *Aquacultural Engineering*, 17, pp.261–272.

O'Toole, C.L., Reed, T.E., Bailie, D., Bradley, C., Cotter, D., Coughlan, J., Cross, T., Dillane, E., Mcevoy, S., Ó Maoiléidigh, N., Prodöhl, P., Rogan, G. and McGinnity, P., 2015. The signature of fine scale local adaptation in Atlantic salmon revealed from common garden experiments in nature. *Evolutionary Applications*, 8(9), pp.881–900.

Scruton, D.A., Pennell, C.J., Robertson, M.J., Clarke, K.D., Eddy, W. and McKinley, R.S., 2005. Telemetry studies of the passage route and entrainment of downstream migrating wild Atlantic salmon (Salmo salar) smolts at two hydroelectric installations on the Exploits River, Newfoundland, Canada. In: M.T. Spedicato, G. Lembo and G. Marmulla, eds. *Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry*. Ustica.pp.91–101.

Steinke, K. and Anderson, J., 2011. *Aquatic PIT tag interrogation system construction and standard operating procedure*. Abernathy.

Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H. and Finstad, B., 2012. A critical life stage of the Atlantic salmon Salmo salar: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*,

81(2), pp.500–542.

Winter, E.R., Tummers, J.S., Aarestrup, K., Baktoft, H. and Lucas, M.C., 2016. Investigating the phenology of seaward migration of juvenile brown trout (Salmo trutta) in two European populations. *Hydrobiologia*, 775(1), pp.139–151.

Zydlewski, G.B., Haro, A., Whalen, K.G. and McCormick, S.D., 2001. Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. *Journal of Fish Biology*, 58(5), pp.1471–1475.

Chapter 4

Spawning-related movements in a salmonid appear timed to reduce exposure to visually-oriented predators

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Abstract

Animals often exhibit extensive flexibility in movement behaviours on a range of temporal and spatial scales in response to cues that predict fitness outcomes. The annual timing of movements between distinct habitats can be crucial, particularly in seasonal environments with narrow ecological windows of opportunity for feeding and breeding. Sexual selection may further shape sex-specific phenology and movement behaviours. Here, we characterised seasonal, daily and diel movement patterns of male and female adult brown trout (*Salmo trutta*) between a lake where they feed and two streams (one inflow and one outflow) where they breed, using passive integrated transponder (PIT) telemetry. Antennae positioned at the inflow and outflow of the lake monitored movements between lake and stream habitats of 186 tagged fish. Across two years in both streams, movements were overwhelmingly nocturnal and exhibited distinct seasonality, with a peak in daily detections close to the winter solstice. In both streams, seasonal movement activity of males began and peaked before that of females. Daily detection probabilities for both sexes increased as the moon waned (decreasing lunar illumination) and as river depth increased, the latter being associated with reduced water clarity. These findings are consistent with fish favouring movement between fluvial and lacustrine habitats when light (both solar and lunar) or hydrological conditions decrease their exposure to visually-oriented predators. The early movement of males relative to females also suggests a role for intrasexual male competition, whereby earlier male arrival in breeding areas could increase mating opportunities.

Introduction

Many species exploit different habitats at various life stages (Werner and Gilliam, 1984), and such ontogenetic niche shifts are particularly prevalent in size-structured populations of insects and fish (Werner and Gilliam, 1984; Claessen and Dieckmann, 2002). Different habitats can yield contrasting opportunities for growth, reproduction, and survival, which may vary with respect to season and the age, maturity or size of an animal. However, movement between habitats often incurs an increased risk of mortality (Lind and Cresswell, 2006) that may vary temporally as environmental conditions change (Schwinn et al., 2017; Jonsson, Jonsson and Jonsson, 2017; Flávio et al., 2019). In areas with distinct seasonal variation, selection tends to promote movement from one habitat to another during an annual period when conditions in the destination habitat are generally favourable for a particular activity such as feeding or reproduction (Åkesson et al., 2017). At a finer temporal scale, selection may promote movement at specific times within the broader migratory period when environmental conditions facilitate the safe passage of migrants or when conditions in the new environment are optimal (Hamilton and Kama, 2004; Hammerschlag et al., 2017).

In areas with pronounced seasonality, species' endogenous circannual rhythms are typically 'entrained' by the cyclical signal of photoperiod, which in turn regulates their seasonal timing at a coarse scale (Åkesson et al., 2017; McCormick, 2012; McNamara et al., 2011). This allows the synchronisation of key life history events such as maturation, migration and reproduction with their long-term average optimum timing (Robart, McGuire and Watts, 2018; Foster, Ebling and Claypool, 1988; Gwinner, 1989; Walton, Weil and Nelson, 2011). Additionally, photoperiodic transitions between darkness and light provide daily signals for entraining circadian

rhythms (Metcalfe, Fraser and Burns, 1998; Hammerschlag et al., 2017). However, variation in other environmental factors such as temperature, tide or rainfall that reliably predict fitness outcomes can provide additional non-photoperiodic signals that allow the timing of behaviours to be fine-tuned within a particular year, season or even day (McNamara et al., 2011; Visser and Both, 2005).

Transitional areas between habitats often represent survival bottlenecks for migratory species, as migrants contend with novel abiotic or biotic challenges such as unfamiliar predators (Dieperink, Pedersen and Pedersen, 2001; Aldvén et al., 2015; Kennedy et al., 2018). For example, predation rates amongst marine turtle hatchlings may exceed 85% as they move the short distance from nesting beach to open water (Whelan and Wyneken, 2007). Many predatory species congregate in such transitional areas at specific times in order to intercept migrating individuals (Quinn and Buck, 2001; Carlson and Quinn, 2007; Bentley et al., 2014; Esbérard and Vrcibradic, 2007). Although predation rates can be exceptionally high during these brief transitional periods, predator efficiency and associated predation rates are often strongly influenced by environmental conditions at the time of migrant passage (Clark & Furey, 2016; McLennan, Rush, Mckelvey, & Metcalfe, 2018; Carlson and Quinn, 2007; Quinn and Buck, 2001). Where predators rely on vision, ambient light levels and environmental clarity will play synergistic roles in determining the distances from which prey are detectable. In response, many prey species limit certain behaviours to times when light levels are low. For example, many birds that are primarily diurnal limit their migratory movements to the hours between sunset and sunrise (Åkesson, Alerstam and Hedenström, 1996; Chernetsov, 2006; Zehnder et al., 2001). Similarly, diel vertical migrations allow zooplankton to descend from

their nocturnal feeding areas near the surface to deeper refuge areas before daylight exposes them to visually-oriented predators (Lampart, 1989; Ohman, 1990).

Light intensity at night, however, is variable and strongly influenced by the lunar cycle. Some species of nocturnal rodents have been found to reduce or cease their foraging activity in exposed areas around full moon and increase such activity around the new moon, probably as a response to nocturnal avian predation (Kotler et al., 1991; Lockard and Owings, 1974; Morrison, 1978). Additionally, visibility in aquatic environments can vary significantly for a given input of lunar or solar light intensity. Such variation in visibility can be particularly pronounced in rivers, where water clarity tends to be associated with variation in discharge because high levels of suspended sediment during high flows often increase turbidity (Doyle et al., 2019). This consequence of increased discharge on the likelihood of migrants being detected by predators is augmented by the increased river volume (and thus reduced density).

In salmonid fishes, migrations between natal streams and more productive feeding areas in lakes, other parts of the river system, or oceans facilitate continued growth and increased fecundity while reducing the influence of density dependent pressures on vital rates (Arostegui and Quinn, 2019; Ferguson et al., 2019; Jonsson and Jonsson, 2011; Nevoux et al., 2019). However, these migrations frequently incur severe mortality costs, often driven by greatly elevated predation rates in transitional habitats such as estuaries (Dieperink, Pedersen and Pedersen, 2001; Aldvén et al., 2015), lakes (Olsson, Greenberg and Eklöv, 2011; Schwinn et al., 2017), and river-to-lake confluences (Kennedy et al., 2018; Carlson and Quinn, 2007; Quinn and Buck, 2001). Thus, there may be strong selection for mature lake-feeding salmonids to limit their pre- and post-spawning movements between lake habitat and natal

streams to periods when environmental conditions reduce predation risk. Previous studies indicate that the behavioural responses of salmonids to temporal variation in environmental conditions can vary markedly amongst populations (Moore et al., 2012; Ovidio, 1999; Ovidio et al., 1998; García-Vega, Sanz-Ronda and Fuentes-Pérez, 2017; Santos et al., 2002; Hellawell, Leatham and Williams, 1974; Rustadbakken et al., 2004; Jonsson, 1991; Jonsson and Jonsson, 2002), suggesting that local adaptations underpin these responses. As such, investigation into the proximate environmental drivers of native salmonid movements in relatively pristine habitats may provide broad insights into the ultimate causes of these behavioural responses.

Across many animal taxa, males and females display differing reproductive migratory phenologies (Tøttrup and Thorup, 2008; Remisiewicz and Wennerberg, 2006). Early arrival at breeding areas relative to the opposite sex can confer contrasting benefits or costs on males and females. These can depend on factors such as physiology (sexual dimorphism), mating system (i.e. monogamous, polyandrous, polygynous etc.), forms of intersexual selection and intrasexual competition, demographics, breeding habitat type and availability as well as any differential in mortality risk associated with habitat or sex (Morbey and Ydenberg, 2001). The early arrival of females relative to males, is generally limited to polyandrous species in which females compete for breeding territory or mates (Rappole, 2013). The early arrival of males relative to females, is more common and is generally associated with polygynous species (Morbey and Ydenberg, 2001). Salmonids represent a particularly interesting group for investigating such sex-based differences in reproductive migratory phenology due to their restricted breeding season, polygamous mating systems (including polygyny and polyandry), often high migrant

and spawning mortality as well as the frequently limited availability of spawning habitat (Gauthey et al., 2015; Montgomery et al., 1999; Morbey, 2002; Nevoux et al., 2019; Quinn, 2018; Serbezov, Bernatchez, Olsen, & Vollestad, 2010; Tappel & Bjornn, 1983).

The aim of this study was to investigate associations between the timing of spawning-related movement of male and female brown trout (between a lake and two spawning streams) and environmental variables that were expected to influence the visibility of migrants to predators. We first investigated whether movement patterns displayed a distinct diel signal associated with periods of daylight or darkness. Secondly, we investigated whether variation in river height and/or moon phase were associated with variation in daily movement patterns and whether these effects were additive or non-additive. Thirdly, we assessed whether males and females displayed differing migratory phenology patterns.

Methods

Study area, fish sampling and behaviour monitoring

Study area

The Burrishoole catchment is a complex freshwater system in the north west of Ireland that drains an area of ~ 83 km^2. A series of streams and rivers link three main lakes, the most elevated and northerly of which is 46 ha Bunaveela Lough (54º 01' 18" N 9º 32' 43" W; maximum depth: 23 m). The lake contains native populations of brown trout (*Salmo trutta* L.), Arctic char (*Salvelinus alpinus* L.), Atlantic salmon (*Salmo salar* L.) and European eel (*Anguilla anguilla* L.). The Fiddaunveela

(hereafter ‘the inflow’) is the only stream flowing into the lake and the Goulaun (hereafter ‘the outflow’) is the outlet (Fig. 1). The inflow rises in the steep hills to the south east of Bunaveela Lough, flowing for approximately 2 km before joining the lake. The outflow meanders to the south west for approximately 10 km prior to joining the larger (410 ha) Lough Feeagh, increasing in width and depth as it gets farther from Bunaveela. During low rainfall periods, most sections of the inflow become shallow and provide limited sheltering habitat for mature-sized (i.e. > 165 mm) salmonids. The water level in the inflow rises and falls rapidly, often within hours of the commencement and cessation of rainfall, whereas the regulating influence of the lake moderates fluctuations in the height of the upper outflow. Both streams are oligotrophic and poorly buffered (hydrological parameters shown Supporting Information Table S1), while small sandstone and limestone deposits help to buffer areas of Bunaveela Lough (Whelan et al., 1998). Long-term records (2005-2018) show that, outside of winter spawning months, < 1% of trout sampled in the inflow (N = 1136) or upper outflow (N = 877) had a fork length (FL) > 165 mm (see Supporting Information Fig. S1), our conservative threshold for designating maturity status (details below). In contrast, more than a quarter of the trout sampled by small mesh beach seine in Bunaveela Lough between 1991 and 2018 (N = 3176) were > 165 mm, indicating that the lake provides a richer feeding habitat, possibly with less exposure to predators, where migrants from the streams can attain greater size prior to spawning.

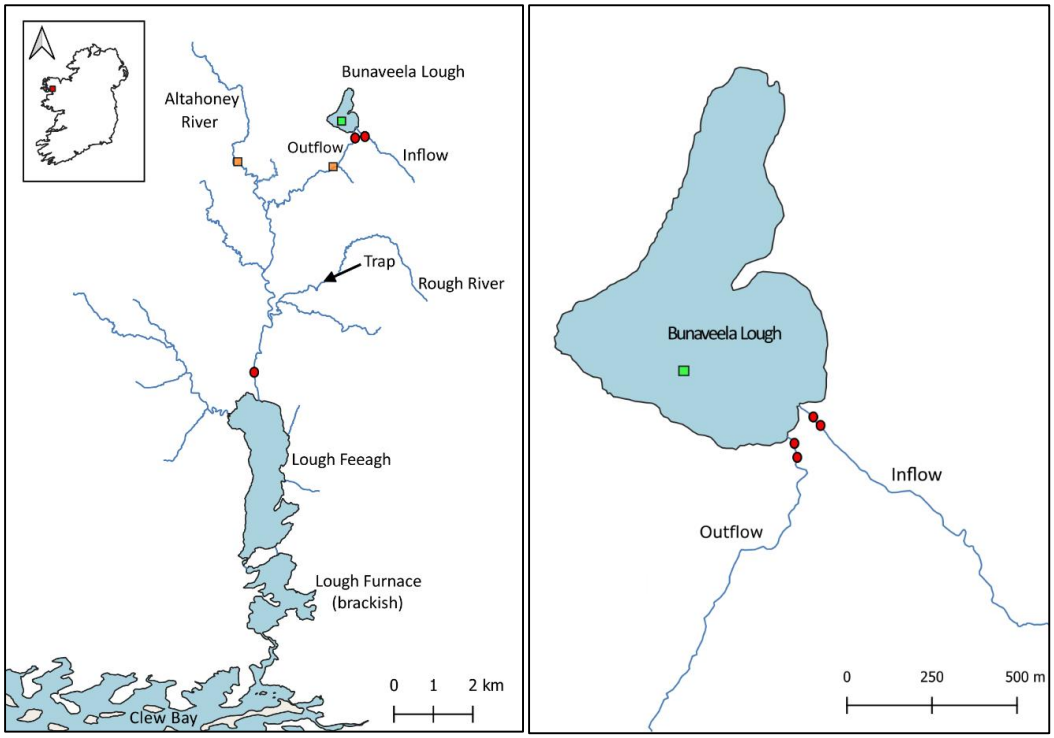


Figure 1. Map of the Burrishoole Catchment and Bunaveela Lough. PIT antennae locations are shown as red circles. Water level logger locations are shown as orange squares. Water temperature logger location is shown as a green square.

Sampling

Between October 2016 and October 2018, seine netting (9 mm half mesh) was used on six dates to capture trout in littoral areas along the south eastern shore of Bunaveela Lough (Supporting Information Table S2). Five hundred trout were captured and anaesthetised in pH-buffered tricaine methanesulphonate (80 mg l^{-1}) before weights (to 0.1 g) and fork lengths (FL, to 1 mm) were measured. A tissue sample (approx. 2 mm^2) was extracted from the tail of each fish and preserved in ethanol (95%) for genetic sex determination. Trout with a FL > 70 mm (N = 456) were tagged with 12 mm passive integrated transponder (PIT) tags. A needle inserted to one side of the mid-ventral line (slightly beyond the tips of the pleural ribs) and

just beyond the tip of the pectoral fin was used to implant tags into the peritoneal body cavity. After tagging, anaesthetised trout were transferred to oxygenated freshwater tanks and observed until they regained their equilibrium and began to swim actively, whereupon they were released back into the lake.

In addition, on three occasions between June and October 2017, we captured trout from eastern shore of Lough Feeagh in the lower section of the catchment (Fig. 1). A fish trap was operated continuously between December 2016 and March 2019 in the Rough River, a spawning river for trout that feed in Lough Feeagh. Trout caught in Lough Feeagh or the Rough River were scanned with a hand held PIT reader, measured and visually inspected to determine their state of maturity. These data were used to inform and support the designation of spawning periods for Bunaveela-caught fish (see below). As with individuals caught in Bunaveela, we PIT-tagged all trout with a FL > 70 mm (N = 1913).

Ethical note

We adhered to the ASAB and ABS guidelines for the treatment of animals in behavioural research throughout this project. We conducted all aspects of sampling and tagging in accord with S.I. No.123/2014 Animal Health and Welfare (operations and procedures) Regulations 2014 and with approval of the Marine Institute animal welfare committee (MI Establishment Authorisation No: AE19121) and the Health Professional Regulatory Authority (HPRA). Procedures for inducing anaesthesia were appropriate for salmonids (Popovic et al., 2012) and full recovery was ensured prior to release. Tagging was carried out by personnel with appropriate training and Individual Authorisations under Scientific Animal Protection Legislation (HPRA).

Genetic sex determination assays

Genomic DNA was extracted from caudal tissue of all tagged trout using the Promega Wizard® SV 96 Genomic DNA Purification System. As described in Finlay et al. (2020) and Keenan et al. (2013), a single sex marker and 18 microsatellite loci were amplified by multiplex PCR (two independent reactions). We determined the genetic sex of each sample depending on whether an amplified DNA fragment of 108 bp was present at the SalmoYF locus (sequence available in GeneBank (P. Prodöhl, unpublished)). This DNA fragment is absent from female brown trout and present in males. In cases where this fragment was absent and three or more of the remaining 18 loci had failed to amplify, sex was designated as 'unconfirmed'.

Monitoring behaviour: PIT telemetry

Between August and September 2017 we constructed and installed and array of four cross-channel, pass-through PIT antennae in the upper Burrishoole catchment (Fig 1.). Such PIT antennae record the time and date that PIT-tagged animals pass antenna locations, allowing individual-based movement patterns to be investigated. We installed two antennae in the upper outflow, 15 m and 30 m downstream of Bunaveela Lough, and two antennae in the lower inflow, 75 m and 85 m upstream from Bunaveela Lough (Fig.1). In order to guarantee that all antennae remained well beyond the edge of lacustrine habitat during the highest water levels, the upper outflow antennae were relocated to 40 m and 60 m downstream of the lake between the first and second spawning periods. In March 2018 we installed a single additional antenna in the lower outflow, 805 m upstream of Lough Feeagh and 9,540 m downstream from Bunaveela Lough (Fig. 1), allowing us to investigate whether

diel movement patterns recorded in the inflow and upper outflow were mirrored in the lower catchment. Each antenna spanned the full depth and width of the channel at its location except during very high flow events. We used a test tag to assess the performance of each antenna every 10 - 14 days and soon after all high flow events. On four occasions during the two spawning periods antennae were found to be damaged by flotsam and were not capable of detecting tags. On each occasion we completed necessary antenna repairs within 48-h of damage occurring, ensuring that antennae functioned efficiently throughout most of the study period. Due to evidence that some tagged trout passed antennae without being detected, directionality of movements (away from the lake or towards it) could not be confidently determined for the majority of PIT-tag detections.

Environmental data

Throughout the study period, a thermistor chain (HOBO Tidbit v2) recorded the water temperature profile of Bunaveela Lough, while an OTT Orpheus Mini Water Level Logger recorded river height in the Altahoney, a tributary of the upper outflow (Fig. 1). In both cases, measurements were taken at 15 min. intervals. A second water level logger operated in the upper outflow (1120 m downstream of Bunaveela Lough) throughout the 2017-2018 spawning period, but was damaged by a flood in February 2018. Concurrent data from the two water level loggers collected over 140 days show that daily mean water heights in the upper outflow and the Altahoney are highly correlated ($R^2 = 0.81$). Additionally, rainfall patterns in the inflow and Altahoney drainage areas, which are less than 2 km apart and occupy similar elevations, are very similar (B. Doyle pers. comm. and Fairman et al., 2017). Thus, the Altahoney water height data were used as proxies for stream height in the inflow

and upper outflow in statistical analyses. The daily water level and water temperature data used in our analyses represent the maximum and mean values respectively that were recorded within a given 24-h period. By using mean daily water level values, discrepancies between the rate of water height fluctuations amongst the three streams should be mitigated.

Measured Altahoney water levels ranged from 0.36 m to 1.54 m (mean = 0.65 m) during the 2017-2018 spawning period and from 0.32 m to 1.50 m (mean = 0.61 m) during the 2018-2019 spawning period. Lake temperature at one meter below the surface ranged from 3.77 °C to 11.07 °C (mean = 6.75 °C) during the 2017-2018 spawning period and from 5.73 °C to 9.06 °C (mean = 7.39 °C) during the 2018-2019 spawning period. Mean lake temperature in the ten days preceding the winter solstice was 5.32 °C in 2017 and 6.73 °C in 2018. The daily timing of sunrise and sunset for the Burrishoole catchment as well as moon phase data are based on data from the United States Naval Observatory (USNO) for 54 º 01’ 18” N 9 º 32’ 43” W. Moon phase is treated as a continuous numerical variable between one (full moon) and zero (new moon). Photoperiod refers to the proportion of the 24-h day that falls between sunrise and sunset, and had a range of 0.307 to 0.373 in both spawning periods (mean = 0.331). Preliminary investigation of PIT-derived data indicated the vast majority of detections during the spawning period occurred at night. In order to avoid splitting discrete nocturnal activity periods at midnight into two separate dates, detection data and environmental data used in our analyses were adjusted so that each 24-hour period began at 12:00 rather than at 24:00.

Defining spawning period, designating mature length threshold and estimating fish length

We used a combination of observational data on the maturity status of trout passing through the Rough River fish trap and PIT-derived data on the movement patterns of Bunaveela-tagged 'mature-sized' trout to designate a spawning migration period for Burrishoole trout, beginning on 1 November and ending on 31 January (see Supporting Information Fig. S2 and results for details). To exclude potentially immature trout from our behavioural analyses, we chose 165 mm as a conservative minimum threshold FL for maturity, as this is roughly one standard deviation below the mean FL of visibly mature (i.e. ripe or spent) brown trout that we captured during the study period (N = 414, mean ± SD = 201.2 ± 36.5 mm). Most (87.6%) of the trout from Bunaveela Lough that were tagged during the project were caught on only the original tagging date. Because trout that were detected on antennae during spawning periods had been tagged up to 811 days previously, the FL of tagged individuals in each spawning period was unknown. Individual growth rates in fish populations are strongly influenced by individual size and water temperature (Neuheimer and Taggart, 2007; Handeland, Imsland and Stefansson, 2008; Boltaña et al., 2017). We therefore used a combination of lake temperature data and individual growth data from 87 individuals that were tagged and recaptured in lake habitat during the project (recapture dates were 15 – 505 days post-tagging) to calibrate a linear model in R v3.6.1 (R Core Team, 2019) to predict growth per growing degree day (GDD) (Chezik, Lester and Venturelli, 2014) as a function of initial FL (full model details and performance indicators presented in Finlay et al. (2020)). We used this model in conjunction with lake temperature and tagging FL data to estimate post-tagging growth, and thus the current FL, for each Bunaveela-

tagged trout in each spawning period. Our growth rate estimates indicate that 243 of the trout we had previously tagged in Bunaveela Lough exceeded 165 mm in length (our designated threshold for maturity) by the 2017-2018 spawning season while 450 of the lake-tagged trout were of mature size by the 2018-2019 spawning period.

Investigating diel movement patterns

All behavioural analyses were conducted using R v3.6.1 and were restricted to the core spawning migration period. To investigate diel movement patterns, all detection timing data were converted to circular format and analyses were carried out with the 'circular' package in R (Agostinelli and Lund, 2017). Kuiper's one-sample test of uniformity on the circle was used to assess whether detection rates in each stream and each spawning period varied throughout the 24-hour day. Diel detection patterns were also assessed for normality using a Watson's goodness of fit test for the von Mises distribution (a circular analogue to a Gaussian distribution). Additionally, the proportion of nocturnal (occurring after sunset and before sunrise) and diurnal (occurring after sunrise and before sunset) detections in each stream in each spawning period were calculated using daily photoperiod data.

Daily movement patterns of individuals in relation to sex and environmental variables

We used a binomial generalized linear mixed model (GLMM), with a logit link function, to explore the extent to which the daily probability of detecting mature-sized lake-tagged trout at the inflow or outflow antennae was associated with four continuous (*Day*, Day^2, *MoonPhase* and *RiverHeight*) and three categorical (*Sex*,

Stream and *Year*) explanatory variables, as well as two-way interactions chosen *a priori* on biological grounds (see below). Models were built with the *glmmTMB* function in the glmmTMB R package (Brooks et al., 2017).

Our response variable was Bernoulli distributed, whereby, for any given date, unique mature fish that were detected in the focal stream (either inflow or outflow) were designated '1', while all mature fish that were not detected in that stream (but were detected in that stream on at least one other occasion during a spawning period) were designated '0'. We included a *RiverHeight*MoonPhase* interaction because moon phase (lunar light level) and river height (turbidity) were predicted to play synergistic roles in determining the visibility of nocturnal migrants to predators. Due to differences in flow direction and availability of shelter habitat between the inflow and outflow, combined with evidence of weak genetic differentiation between the groups of trout that spawn in them (Finlay et al., 2020), we predicted that behavioural responses to environmental cues in each stream might differ, and therefore we included two-way interactions between *Stream* (a two-level categorical variable corresponding with 'inflow' and 'outflow') and both *MoonPhase* and *RiverHeight*. We also included two-way interactions between *Sex* and *MoonPhase*, *Sex* and *RiverHeight* and *Sex* and *Day* under the expectation that males and females might exhibit differing migratory phenologies (i.e. protandry or protogyny) or behavioural responses to stochastic environmental cues. *TagNumber* (the individual PIT tag ID of each fish) was included as a random effect (intercept) in our models to account for repeated measures of individual fish throughout the study period, while *Year* was treated as a two-level fixed effect corresponding to the 2017-18 and 2018-19 spawning periods.

Prior to model fitting**,** we used the *scale* function in R to mean-centre and scale all continuous main effects to standard deviation units and we quantified collinearity amongst all fixed effects by Pearson's R using the *cor.test* function in R. Additionally, the variance inflation factors (VIFs) of all fixed effects were calculated with the *check_collinearity* function in the performance R package (Lüdecke, Makowski and Waggoner, 2019). We used the 'DHARMa' package (Hartig, 2019) to plot fitted values vs simulated (scaled) residuals to test for heteroscedasticity and violations of linearity assumptions, and we used the acf function in the *stats* R package to identify residual temporal autocorrelation. The conditional and marginal R^2 of the model were estimated using the *r.squaredGLMM* function in the MuMIn R package (Barton, 2019). Using our model, we employed the *ggPredict* function in the ggeffects R package (Lüdecke, 2018) to plot predicted relationships of interest.

To further investigate sex-based variation in spawning phenology, the first, last and median detection dates, as well as the total number of detection dates and the mean number of detections per detection date were calculated for each fish in each stream (and in both streams combined) in each spawning period. These data were used to summarise overall and sex-specific detection patterns in both streams for both spawning periods (Table 1). Mann-Whitney tests were used to test for sex-based differences in the first detection date and the number of dates during which individual fish were detected in each stream in each spawning period.

Results

Tag detections

More than 95 % of annual detections from mature-sized trout were recorded on our fluvial antennae and more than 95 % of visibly mature ('ripe') trout were caught in the Rough River traps within the designated spawning period (Supporting Information Fig. S2 and Table S3), indicating that movement between lakes and rivers during this period is motivated principally by breeding rather than exploratory foraging. Over the two spawning periods, our fluvial antennae detected 197 trout that were designated as mature at the time of detection, producing in excess of 100 000 detections. Of these fish, 106 were detected in the 2017-2018 spawning period (56 in the inflow, 86 in the outflow and 36 in both), 116 were detected during the 2018-2019 spawning period (51 in the inflow, 89 in the outflow and 24 in both), and 25 were detected in both spawning periods. Sex was confidently determined for 441 of the 456 trout that were PIT tagged in Bunaveela Lough during the study period (190 (43.1%) and 251 females (56.9%)). Over the two spawning periods, 80 mature females and 110 mature males were detected on our fluvial antennae, including 11 individuals of each sex that were detected in both spawning periods. Seven trout of unconfirmed sex were also detected (three in both spawning periods) but these individuals were excluded from the GLMM.

Characterising seasonal movement patterns

Daily movement activity, expressed both as the number of mature-sized lake-tagged trout detected by fluvial antennae (Fig. 2) and as the total number of detections

generated by such fish (Supporting Information Fig. S2), was low between February and October, rose rapidly in November and peaked around the winter solstice before declining rapidly in January. Activity levels in the inflow fluctuated considerably from day to day**,** while changes in activity levels in the outflow were generally more gradual. Substantial increases in activity patterns appeared to often coincide with the new moon or with elevated river height (Fig. 2).

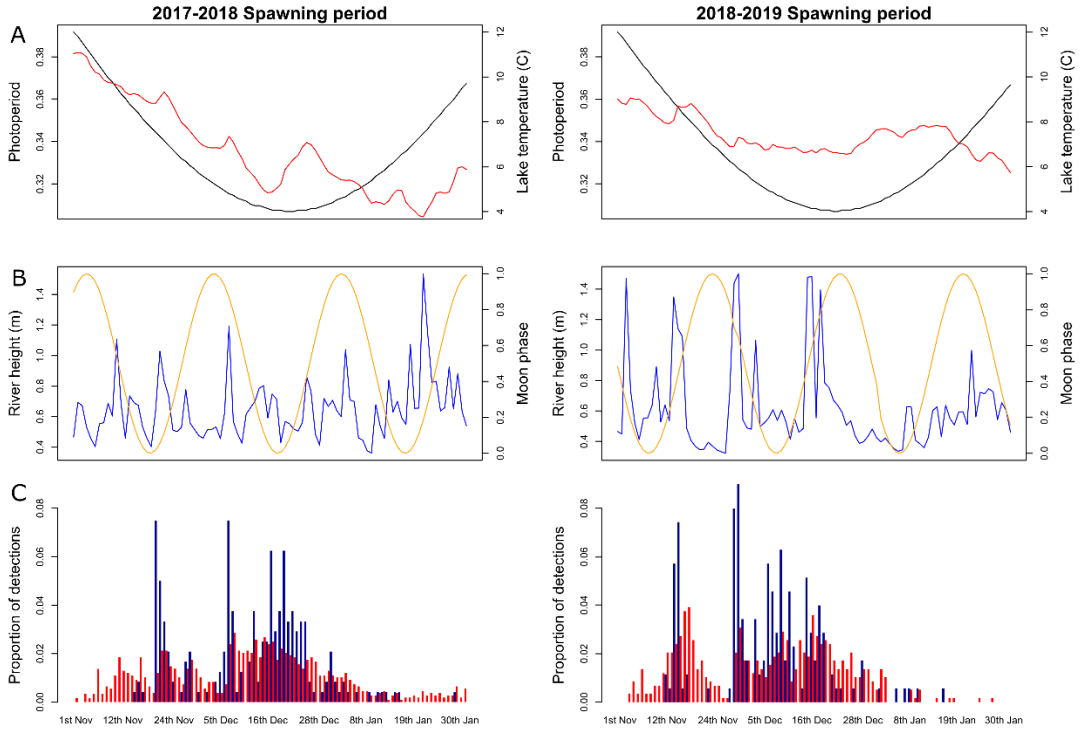


Figure 2. (A) Daily variation in photoperiod (i.e. proportion of the day between sunrise and sunset) (black) and lake temperature (red). (B) Daily variation in water height in the Altahoney stream (blue) and moon phase (yellow). Full moon = 1, new moon = 0. (C) Daily variation in the number of fish detected in the inflow (blue) and outflow (red) streams in each spawning period as a proportion of the total number detected in each stream in the relevant spawning period.

Investigating diel movement patterns

The distributions of diel detections were non-uniform (Kuiper's test: all $P < 0.01$) and non-von Mises distributed (Watson test: < value nearest to critical in all cases) in both streams and both spawning periods. During the 2017-2018 season, 95.6% and 96.7% of detections from mature-sized trout in the inflow and the upper outflow respectively occurred after sunset and before sunrise (Fig. 3). Similarly, during the 2018-2019 season, 88.6% and 92.7% of detections from mature-sized trout in the inflow and the upper outflow respectively occurred after sunset and before sunrise. The antenna at the transition into Lough Feeagh recorded a comparable nocturnal bias (96.9%) during the 2018-2019 spawning season.

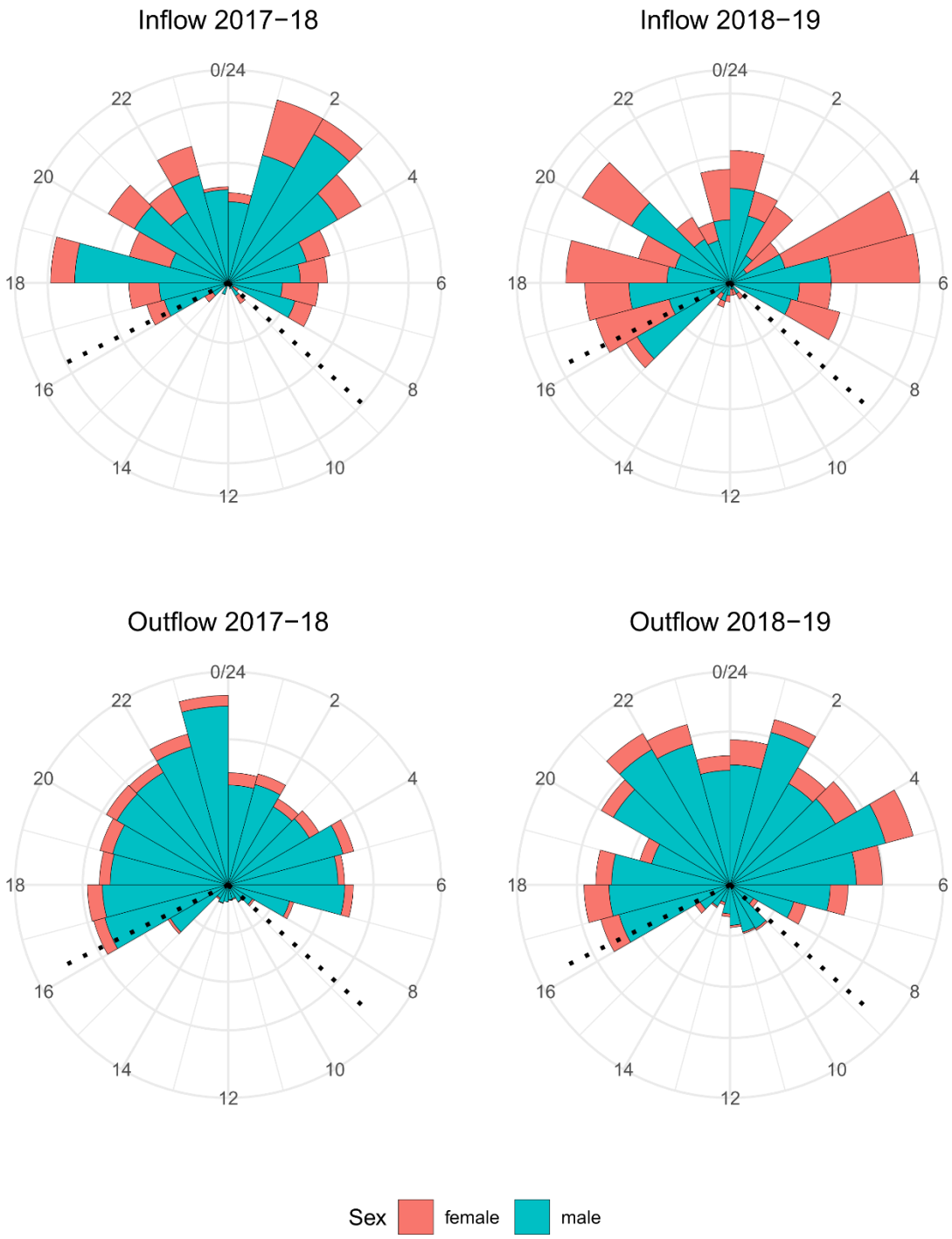


Figure 3. Diel distribution of detections (hourly) from mature male and female trout recorded on the inflow and outflow antennae during the two spawning periods. Male and female bars sum to 100%. The dotted black lines represent sunrise (08:52) and sunset (16:15) on the median day of each spawning period.

Daily movement patterns of individuals in relation to sex and environmental variables

All correlations between fixed effect covariates in our movement probability model were well below R=0.7, and all model parameter VIFs were < 10. Model validation confirmed that the model complied with all underlying assumptions, including no evidence of residual temporal autocorrelation.

Detection probability increased as *RiverHeight* increased and as *MoonPhase* decreased (Table 2, Fig. 4). A significant two-way interaction effect was found between *RiverHeight* and *MoonPhase* ($P < 0.001$), whereby the negative effect of *MoonPhase* became less pronounced at higher *RiverHeight* values (Table 2), but this interaction was relatively weak and less pronounced in the inflow river (Fig. 4). Fish detection probabilities were higher overall in the outflow river (Table 2, Fig. 4), but the positive effect of *River Height* and the negative effect of *MoonPhase* were both weaker in the outflow river ($P < 0.001$ for both *Stream* × *RiverHeight* and *Stream* × *MoonPhase* interactions; Table 2, Fig. 4).

There was a significant quadratic effect of *Day*, with an *n*-shaped curve (Fig. 5; Table 2). The main effect of *Day* was also significant, indicating that detections did not peak at *Day* zero, where zero corresponded to the median date (15th of December) within the spawning season as *Day* was mean centred. Detection probability was significantly higher for males than for females, and their detection probabilities peaked significantly earlier (*Sex* × *Day* interaction, $P < 0.001$; Table 2, Fig. 5). However, detection probability for males was less strongly associated with water height than that of females (*Sex* × *RiverHeight* interaction, $P = 0.044$). The *Sex* × *MoonPhase* interaction was not significant ($P = 0.58$). Detection probabilities were significantly higher in the first spawning period than the second (Table 2; Fig.

5). Overall, 44% of the variation in detection probability was explained by a combination of the fixed and random effects (i.e. conditional R^2) in our GLMM, while fixed effects alone (i.e. marginal R^2) explained 31%. Thus, the random effect of *TagNumber* accounted for 13% of the overall variation.

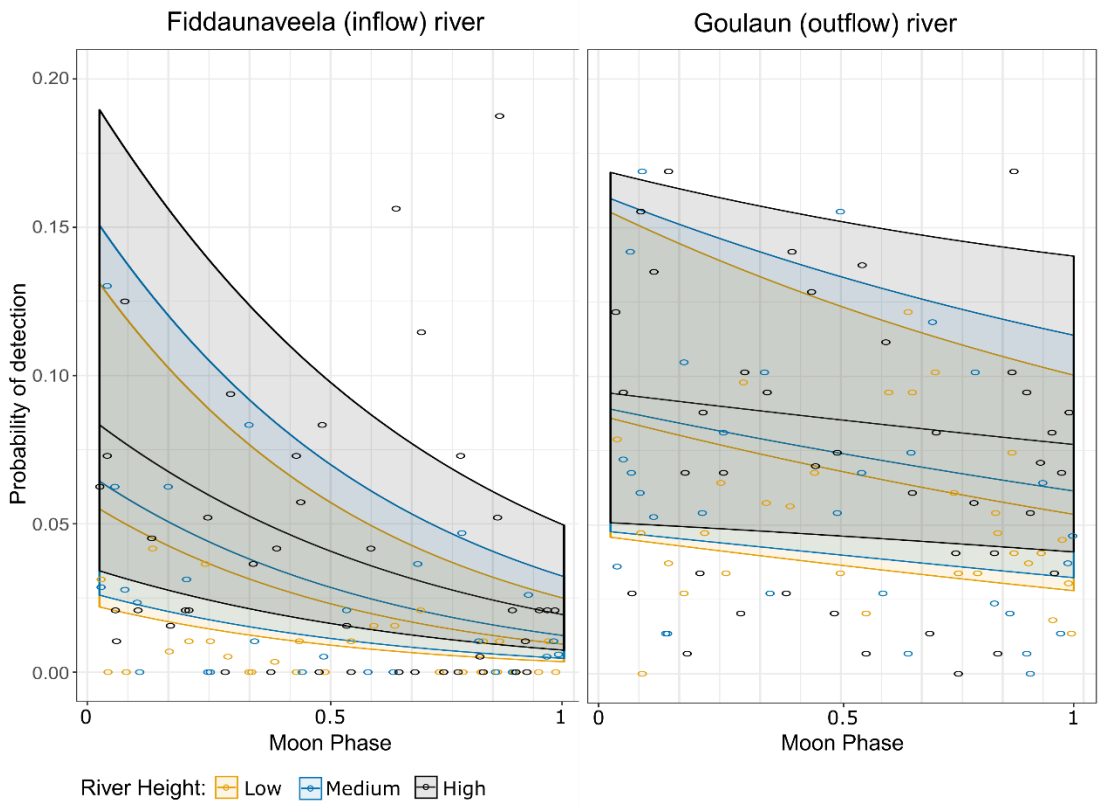


Figure 4. Detection probability of mature trout in the inflow and outflow in relation to moon phase at low (orange), medium (blue) and high (black) river heights as predicted from the GLMM. Shaded areas represent 95% confidence intervals.

Table 1. Summary of individually-based detection data split by sex, stream and spawning period. **N** is the number of fish per group. **First Dtn.**, **Last Dtn.** and **Median Dtn.** are mean dates ± SD (in days) generated from the first, last and median dates on which each fish in each group was detected. # **Days** is the mean number of separate dates on which each fish in each group was detected. **Dtns per Day** is the mean number of detections generated by each fish in each group on each date that they were detected. Row names ending in '**Earlier**' designate how much earlier, in days, the named group is compared to the opposite group. Rows marked with an asterisk use all detection data, regardless of stream. Group names containing '(**All Fish**)' include males, females and individuals for which sex could not be confidently determined. Some individuals were detected in both streams during a single spawning period and some individuals received no sex designation (described in Results above), causing the number of fish in group totals to differ from the apparent sum of the fish in their constituent groups.

	2017-2018 Spawning Period						2018-2019 Spawning Period					
Group	**N**	**First Dtn.**	**Last Dtn.**	**Median Dtn.**	**# Days**	**Dtns per Day**	**N**	**First Dtn.**	**Last Dtn.**	**Median Dtn.**	**# Days**	**Dtns per Day**
Inflow (All Fish)	56	04 Dec ±15.8	18 Dec ±15.1	11 Dec ±13.8	4.1 ±4.4	3.1	51	27 Nov ±16.5	08 Dec ± 15.9	03 Dec ±14.9	2.9 ±2.8	3.1
Outflow (All Fish)	86	29 Nov ±22.8	25 Dec ±25.6	12 Dec ±20.3	12.6 ±14.1	34.9	89	29 Nov ±23.6	18 Dec ± 22.7	08 Dec ±2.4	6.6 ±6.3	7.9
Outflow Earlier		**4.0**	**-8.0**	**-2.0**				**-2.00**	**-10.0**	**-5.0**		
Male (Both streams)*	62	24 Nov ±22.0	26-Dec ±25.9	10 Dec ±20.0	15.3 ±15.2	29.2	59	19 Nov ±18.3	08 Dec ±20.1	29 Nov ±18.2	8.0 ±7.5	8.7
Female (Both Streams)*	40	05 Dec ±21.3	25 Dec ±23.2	15 Dec ±19.9	7.3 ±7.2	11.3	51	06 Dec ±21.6	24 Dec ±19.3	15 Dec ±18.2	4.8 ±3.5	3.2
Male Earlier		**12.2**	**-0.1**	**6.1**				**16.3**	**15.7**	**16.0**		
Inflow Male	37	01 Dec ±14.4	15 Dec ±14.2	08 Dec ±12.5	4.4 ±4.7	3.3	24	21 Nov ±13.9	03 Dec ± 15.1	27 Dec ±13.3	3.8 ±2.8	3.5
Inflow Female	17	11 Dec ±16.9	25 Dec ±15.4	18 Dec ±14.6	3.3 ±2.5	2.7	23	05 Dec ±16.4	15 Dec ± 14.6	10 Dec ±14.0	2.5 ±1.6	2.6
Inflow Male Earlier		**9.9**	**10.3**	**10.1**				**13.6**	**12.1**	**12.8**		
Outflow Male	47	25 Nov ±23.2	29 Dec ±26.3	12 Dec ±20.2	17.2 ±16.3	49.5	47	22 Nov ±20.3	11 Dec ±21.6	01 Dec ±19.7	8.2 ±7.5	11.3
Outflow Female	35	05 Dec ±21.3	23 Dec ±23.6	14 Dec ±20.2	6.9 ±7.4	15.4	37	07 Dec ±23.2	26 Dec ± 20.9	16 Dec ±19.6	5.0 ±3.7	3.5
Outflow Male Earlier		**10.8**	**-5.7**	**2.6**				**14.8**	**15.3**	**15.0**		
Total (All Fish)*	106	28 Nov ±22.2	25 Dec ±24.5	12 Dec ±19.9	12.1 ±13.1	25.8	116	27 Nov ±21.3	16 Dec ±21.8	06 Dec ±19.7	6.5 ±6.2	6.2

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Table 2. Parameter estimates for the main effects and interaction effects from the binary GLMM, where daily binary detection probability of fish was the response variable. All estimates and their standard errors are on the logit scale and therefore correspond to log odds ratios. The odds ratio is also given (exponent of logit-scale parameter estimates), as well as the 5% and 95% confidence intervals around this. The intercept corresponds to mean values on the logit scale for females in the inflow river in the first spawning period (the reference levels for *Sex* and *Stream* and *Year*) when all continuous covariates are set to zero.

Effect	Estimates	Std. Error	z value	Odds ratio	5%	95%	P value
(Intercept)	-3.863	0.137	-28.299	0.021	0.017	0.026	<0.001
RiverHeight	0.629	0.053	11.815	1.875	1.718	2.047	<0.001
MoonPhase	-0.552	0.077	-7.211	0.576	0.508	0.653	<0.001
Stream (Outflow)	1.249	0.086	14.583	3.486	3.028	4.013	<0.001
Sex (Male)	0.424	0.149	2.841	1.528	1.196	1.954	0.005
Year (Second)	-0.688	0.053	-13.028	0.503	0.461	0.548	<0.001
Day	-0.28	0.062	-4.538	0.756	0.683	0.837	<0.001
Day^2	-0.737	0.037	-19.768	0.479	0.450	0.509	<0.001
RiverHeight × *MoonPhase*	0.108	0.031	3.448	1.114	1.058	1.172	<0.001
RiverHeight × *Stream (Outflow)*	-0.357	0.049	-7.259	0.700	0.646	0.759	<0.001
MoonPhase × *Stream (Outflow)*	0.433	0.070	6.189	1.542	1.374	1.730	<0.001
RiverHeight × *Sex (Male)*	-0.094	0.046	-2.016	0.911	0.844	0.983	0.044
MoonPhase × *Sex (Male)*	0.032	0.058	0.558	1.033	0.940	1.135	0.577
Sex (Male) × *Day*	-0.619	0.075	-8.273	0.54	0.476	0.610	<0.001
TagNumber (Random Effect)				2.396	2.192	2.644	

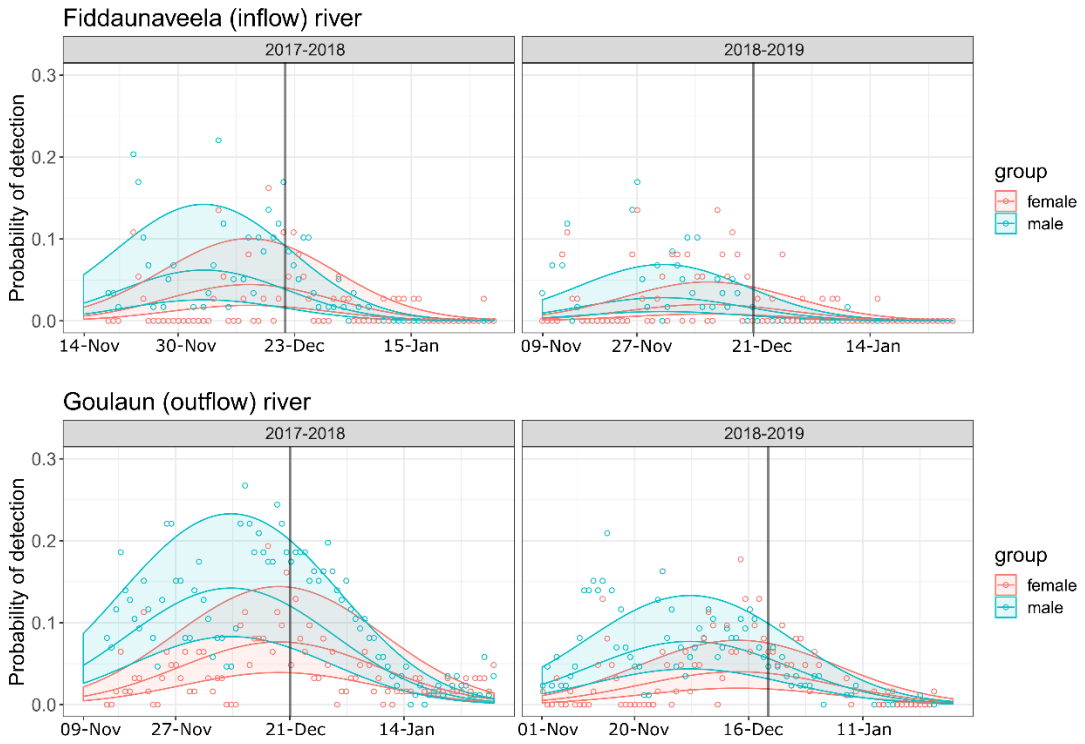


Figure 5. Temporal variation in detection probability of males (blue) and females (orange) in both streams and both spawning periods as predicted from the GLMM. Shaded areas are 95% confidence intervals. Dark vertical line represents the winter solstice.

Across both streams, the mean first detection date amongst male migrants was 12 and 16 d earlier than that of female migrants in the 2017-2018 and 2018-2019 spawning periods respectively, while the mean last detection of males was 0.1 day later and 16 days earlier than that of females (Table 1). The difference between male and female first detection dates was significant in both streams in both study seasons (Mann-Whitney tests: $W = 429.5 – 1278$, all $P < 0.05$). Individual males were detected in the outflow on significantly more dates than individual females in the first (Mann-Whitney test: $W = 562.5$, $P = 0.014$) but not second (Mann-Whitney test: $W = 690.5$, $P = 0.106$) spawning period, and corresponding sex differences were not

significant in the inflow in either spawning period (Mann-Whitney test: W = 243.5, P = 0.66 and W = 145.5, P = 0.10). Furthermore, on each date during which they were detected in the outflow during the 2017-2018 and 2018-2019 spawning periods respectively, individual males produced 3.2 and 3.2 times as many separate detections as individual females produced (49.4 vs 15.4 and 11.3 vs 3.5). In the inflow, the average number of detections produced per male per 'active' date in 2017-2018 and 2018-2019 respectively was 1.2 and 1.3 times higher than that of females (3.3 vs 2.7 and 3.5 vs 2.6).

Discussion

This study provides evidence that the timing of spawning-related movements of brown trout between lake habitat and spawning streams is strongly associated with environmental factors that are likely to influence their visibility to potential predators. In both streams and in both spawning periods, most (~89-97%) detections from mature-sized trout were recorded between sunset and sunrise, indicating a strong and consistent tendency to through transitional lake-to-river habitat at night (Fig. 3). The antenna located close to the confluence with Lough Feeagh (Fig. 1) recorded a similar (96.9%) nocturnal bias, suggesting that nocturnal spawning movements through transitional habitat may be prevalent within the Burrishoole catchment. It is generally believed that nocturnally-biased migration in salmonids represents a strategy to minimise migrant visibility and exposure to diurnal predators (Bradford and Higgins, 2001; Ovidio et al., 2002; Zavorka et al., 2016; Fraser et al., 1995; Ibbotson et al., 2006; Thorstad et al., 2012). In support of this, Flavio *et al.* (2019) found that Atlantic salmon smolts conducting nocturnal movements between fluvial and marine habitats had significantly higher survival than those that moved

during the day. While nocturnal spawning migrations are found in some brown trout populations (Ovidio, 1999; Ovidio et al., 1998; Piecuch et al., 2007; Moore et al., 2012) they are not ubiquitous (García-Vega, Sanz-Ronda and Fuentes-Pérez, 2017; Santos et al., 2002), suggesting that the advantages conferred by this behaviour are context specific. Indeed, some populations appear to alternate between nocturnally and diurnally biased spawning migrations at low and high river heights respectively (Rustadbakken et al., 2004; Hellawell, Leatham and Williams, 1974). For the trout that feed in Bunaveela, moving from a deep lake habitat to shallow stream habitat is likely to alter predation risk and, in particular, increase exposure to grey herons (*Ardea cinerea*) and Eurasian otters (*Lutra lutra*). Previous studies have recorded high predation rates of salmonids during spawning migrations by both otters and herons (Carss, Kruuk and Conroy, 1990; Pépino, Rodríguez and Magnan, 2015) and, on numerous occasions during the two spawning periods, herons were observed at dusk hunting in the shallow riffles close to our PIT-antennae where the inflow and outflow connect to the lake (R. Finlay, pers. obs.). Future work could confirm or refute these conjectures with direct measures of predation risk and relate these to direct measures of ambient light levels, which, for example, could be affected by cloud cover.

Seasonal movements of mature trout in our study (PIT detections and Rough River trap captures) peaked close to the winter solstice in both years despite differing prevailing water temperatures (Fig. 2 and Supporting Information Fig. S2), suggesting that photoperiod plays a dominant role in entraining local spawning phenologies. The unambiguous date signal provided by photoperiodic variation has previously been shown to drive the broad seasonal phasing of reproduction in salmonids, as well as physiological developments associated with sexual maturation

(Billard, Reinaud and Le Brenn, 1981; Bromage, Porter and Randall, 2001; Pankhurst and King, 2010). Locally-adapted responses to photoperiodic variation allow populations to spawn at a time that, on average, maximises fitness (Foster, Ebling and Claypool, 1988; Gwinner, 1989; Quinn, Unwin and Kinnison, 2000; Robart, McGuire and Watts, 2018; Walton, Weil and Nelson, 2011). Selection for an optimal emergence date of offspring is likely to play a central role in determining the optimal spawning time of the parents, in addition to direct selective pressures on the adults (Crozier et al., 2008). Synchrony with the winter solstice is probably coincidental in our case; that is, in this particular system, reproductive success may on average be highest for fish that undertake spawning movements in mid to late December.

The associations we document between daily movement probability and environmental variables (*RiverHeight* and *MoonPhase*) indicate that, in addition to photoperiodic responses, brown trout exhibit phenotypic plasticity in movement behaviours that may allow them to balance anticipated benefits of moving on a particular day against perceived mortality risk. Specifically, trout displayed a significant reduction in the frequency of their movements through transitional habitat when stream height was low and when the moon was full (Fig. 4). These patterns were particularly pronounced in the inflow, the shallower of the two streams, which also provides less sheltering habitat than the outflow. While increases in stream height may facilitate the rapid passage of migrants through risky areas such as shallow riffles (Carss, Kruuk and Conroy, 1990), they also provide a less confined habitat in which to avoid predation and tend to be associated with a reduction in migrant visibility through increased water colour (Doyle et al., 2019), depth, and turbidity. In keeping with our finding that stream height correlated more strongly

with movement in the inflow, previous research indicates that salmonids use increased flow as a cue for upstream migration most frequently in small or shallow streams and rivers (Jonsson, 1991), while in large or deep rivers, increased flow may have a negligible (Hellawell, Leatham and Williams, 1974; Rustadbakken et al., 2004), or even negative (Jonsson and Jonsson, 2002) effect on spawning-related migratory activity.

The apparent reluctance of the lake-tagged trout to move through transitional habitat around the full moon reflects Slavik et al.'s (2012, 2018) observation of trout moving smaller distances during the full than the new moon. Analogous patterns of reduced activity or presence within exposed habitats during the full moon have been recorded in terrestrial rodents (Kotler, Brown and Hasson, 1991; Lockard and Owings, 1974; Daly et al., 1992), catadromous eels (Poole, Reynolds and Moriarty, 1990; Sandlund et al., 2017), marine fishes (Hammerschlag et al., 2017), bats (Morrison, 1978), armadillos (Pratas-Santiago et al., 2017), ungulates (Palmer et al., 2017) and zooplankton (Last et al., 2016). Such 'lunar phobia' is regarded as an evolved response that reduces exposure to visually-oriented predators. Nocturnal activity patterns (Cozzi et al., 2012), detection range and hunting efficiency (Robinson and Tash, 1979; Fraser and Metcalfe, 1997; Metcalfe, Valdimarsson and Fraser, 1997) of visually-oriented predators tend to decline significantly as lunar illumination levels decrease. Although moving during the new moon is likely to reduce migrant visibility and predation rates, it is also possible that nocturnal spawning during the new moon provides a fitness advantage by reducing egg predation by other fish (Šmejkal et al., 2018; Hammerschlag et al., 2017).

We detected a significant interaction between *RiverHeight* and *MoonPhase*, whereby the reduction in movement probabilities at higher values of *MoonPhase* (fuller

moons) was more pronounced when water levels were lower. This interaction makes sense in the context of fish avoiding moving when predation risk is highest, as it suggests that, as the full moon approaches, fish are even more reluctant to move when the water is low and clear with minimal turbidity. However, the effect size was small and was weaker in the inflow stream, so we are reluctant to attach much interpretive weight to this interaction other than to note that it is consistent with our overall conjecture that spawning-related movement decisions may be adapted to reduce predation risk.

Our statistical model and our individual-based summary data (Table 2 and Table 1) revealed significant sex-related differences in spawning phenology that were consistent with protandry (*sensu* Morbey, 2000; i.e. the early arrival of males). In both streams and spawning periods, male detection probability peaked ~12-14 days before that of females (Fig. 5) and individual males tended first move between 10 and 15 days before individual females (Table 1). Protandry has previously been recorded in both Pacific and Atlantic salmonid species (Esteve, 2005; Jonsson & Jonsson, 2011; Morbey, 2000; Quinn, 2018), although the requirement for iteroparous species, such as brown trout, to preserve sufficient energy to survive spawning may place size-dependent constraints on the magnitude or degree of protandry (Morbey, 2002). Such a trade-off may help explain why Seamons et al. (2004) did not detect protandry in iterparous steelhead (*Oncorhynchus mykiss*), despite females mating almost exclusively with males that arrived at spawning areas before them.

The mate opportunity hypothesis, whereby earlier arrival of polygynous males at breeding areas increases their opportunity to mate with females, is a plausible explanation for protandry in salmonids, particularly in populations where males

reproduce for a longer period than females (Anderson et al., 2013; Fenkes et al., 2016; Aarestrup and Jepsen, 1998; Morbey, 2000). However, given that we found limited evidence for a longer reproductive period amongst males in the focal populations (Table 1), it is also possible that selection on females acts similarly, favouring relatively late arrival in order to ensure that males are present in sufficient numbers to promote intrasexual competition amongst males while increasing mate choice and decreasing waiting costs for females (Morbey and Ydenberg, 2001). A third potential explanation is that early arriving males enjoy a rank advantage, establishing territorial dominance before the arrival of later males. However, male salmonids tend to roam extensively during spawning while females compete for prime spawning territory (Carss, Kruuk and Conroy, 1990; Nevoux et al., 2019), suggesting that rank advantage mechanisms could also promote early arrival of females.

Individual males were generally more active during the spawning period compared to females, particularly in the outflow stream, as evidenced by a higher mean number of detection days per male and more detections per day (Table 1). Male detection span (i.e. the period between first and last detections) and frequency in the outflow were also substantially higher in the first than the second spawning period. The outflow antennae were positioned closer to the lake in the first period compared to the second, which may have resulted in increased detections of males conducting short-distance exploratory movements into the outflow in search of females. In contrast with inflowing streams, olfactory cues (i.e. female pheromones) from outflows are unavailable to fish in lakes, requiring males to physically enter outflowing streams in order to confirm the presence of ripe females.

Salmonids can sometimes shed intraperitoneal PIT tags when spawning (Prentice, Flagg and McCutcheon, 1990; Bateman, Gresswell and Berger, 2009), and it has been speculated that such shedding is more common in females. However, the similar span between first and last detection dates of individual males and females in three out of four stream-year combinations (Table 1), coupled with the identical number of males and females that were detected in both spawning seasons (11 of each sex), suggests that tag-shedding did not occur more frequently amongst females.

The male-biased detection frequency patterns found in this study are in keeping with Evan's (1994) observation that male anadromous brown trout will leave and re-enter spawning rivers repeatedly within a spawning season while females generally return rapidly to the ocean after their eggs are laid. Such behavioural differences may increase predation risk for males. Indeed, Carss *et al.* (1990) observed considerably higher predation by otters on male than female Atlantic salmon during the spawning period and speculated that this male-bias was largely due to the vulnerability of males as they move through shallow riffles during their extensive upstream and downstream excursions. The lack of evidence for differing responses to stream height or moon phase by male and female trout in our current study was somewhat surprising, however. The overall lower activity of females compared with males, in conjunction with evidence of females responding more to variation in stream height (Table 2), is in keeping with Belding's (1934) and Fleming's (1996) assertion that during the spawning season, female salmonids tend to be more risk averse than males.

Conclusions

In this study we documented pronounced seasonality and sex-differences in spawning movement behaviours in brown trout that likely reflect inherited phenology patterns that are cued, at a coarse scale, by photoperiod. At a finer scale, trout appear to move between lacustrine and stream habitats at times that minimise their exposure to visually-oriented predators, by moving at night and during darker lunar conditions and higher flows. These findings may be relevant from a conservation perspective, in that climate change or other anthropogenic factors such as artificial light or flow regulation may interfere with the signals fish use to time key transitions between habitats, or lead to mismatches between cue and selective environment, with consequences for fitness.

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References

Aarestrup, K. and Jepsen, N., 1998. Spawning migration of sea trout (Salmo trutta (L)) in a Danish river. *Hydrobiologia*, 371, pp.275–281.

Agostinelli, C. and Lund, U., 2017. *Circular Statistics (version 0.4-93)*.

Åkesson, S., Alerstam, T. and Hedenström, A., 1996. Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. *Journal of Avian Biology*, 27, pp.95–102.

Åkesson, S., Ilieva, M., Karagicheva, J., Rakhimberdiev, E., Tomotani, B. and Helm, B., 2017. Timing avian long-distance migration: From internal clock mechanisms to global flights. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1734).

Aldvén, D., Hedger, R., Økland, F., Rivinoja, P. and Höjesjö, J., 2015. Migration speed , routes , and mortality rates of anadromous brown trout S almo trutta during outward migration through a complex coastal habitat. *Marine Ecology Progress Series*, 541, pp.151–163.

Anderson, J.H., Faulds, P.L., Atlas, W.I. and Quinn, T.P., 2013. Reproductive success of captively bred and naturally spawned Chinook salmon colonizing newly accessible habitat. *Evolutionary Applications*, 6, pp.165–179.

Arostegui, M.C. and Quinn, T.P., 2019. Reliance on lakes by salmon, trout and charr (Oncorhynchus , Salmo and Salvelinus): An evaluation of spawning habitats, rearing strategies and trophic polymorphisms. *Fish and Fisheries*, 20(4), pp.775–794.

Barton, K., 2019. *MuMIn: Multi-Model Inference. R package version 1.43.6.*

Bateman, D.S., Gresswell, R.E. and Berger, A.M., 2009. Passive Integrated Transponder Tag Retention Rates in Headwater Populations of Coastal Cutthroat Trout Passive Integrated Transponder Tag Retention Rates in Headwater Populations of Coastal Cutthroat Trout. *North American Journal of Fisheries Management*, 29, pp.653–657.

Belding, D.L., 1934. The Spawning Habits of the Atlantic Salmon. *American Fisheries Society*, 64, pp.211–218.

Bentley, K.T., Schindler, D.E., Cline, T.J., Armstrong, J.B., Macias, D., Ciepiela, L.R. and Hilborn, R., 2014. Predator avoidance during reproduction: Diel movements by spawning sockeye salmon between stream and lake habitats. *Journal of Animal Ecology*, 83(6), pp.1478–1489.

Billard, R., Reinaud, P. and Le Brenn, P., 1981. Effects of changes of photoperiod on gametogenesis in the rainbow trout (Salmo gairdneri). *Reproduction Nutrition Développement*, 21(6A), pp.1009–1014.

Boltaña, S., Sanhueza, N., Aguilar, A., Gallardo-escarate, C., Arriagada, G., Valdes, J.A., Soto, D. and Quiñones, R.A., 2017. Influences of thermal environment on fish growth. *Ecology and Evolution*, 7, pp.6814–6825.

Bradford, M.J. and Higgins, P.S., 2001. Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Oncorhynchus mykiss). *Canadian Journal of Fisheries and Aquatic Science*, 58, pp.365–374.

Bromage, N., Porter, M. and Randall, C., 2001. The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. *Aquaculture*, 197(1–4), pp.63–98.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M. and Bolker, B.M., 2017. {glmmTMB} Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, 9(2), pp.378–400.

Carlson, S.M. and Quinn, T.P., 2007. Ten years of varying lake level and selection on size-at-maturity in sockeye salmon. *Ecology*, 88(10), pp.2620–2629.

Carss, D.N., Kruuk, H. and Conroy, J.W.H., 1990. Predation on adult Atlantic salmon, Salmo salar L., by otters, Lutra lutra (L.), within the River Dee system, Aberdeenshire, Scotland. *Journal of Fish Biology*, 37, pp.935–944.

Chernetsov, N., 2006. Habitat selection by nocturnal passerine migrants en route : mechanisms and results. *Journal of Ornithology*, 147, pp.185–191.

Chezik, K.A., Lester, N.P. and Venturelli, P.A., 2014. Fish growth and degree-days II: selecting a base temperature for an among-population study. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(9), pp.1303–1311.

Claessen, D. and Dieckmann, U., 2002. Ontogenetic niche shifts and evolutionary branching in size-structured populations. *Evolutionary Ecology Research*, 4(2), pp.189–217.

Clark, T.D. and Furey, N., 2016. Tracking wild sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and high mortality. *Ecological Applications*, 26(4), pp.959–978.

Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A. and Macdonald, D.W., 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, 93(12), pp.2590–2599.

Crozier, L.G., Hendry, A.P., Lawson, P.W., Quinn, T.P., Mantua, N.J., Battin, J., Shaw, R.G. and Huey, R.B., 2008. Potential responses to climate change in organisms with complex life histories : evolution and plasticity in Pacific salmon. *Evolutionary Applications*, 1(2), pp.252–270.

Daly, M., Behrends, P.R., Wilson, M.I. and Jacobs, L.F., 1992. Behavioural modulation of predation risk : moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, Dipodomys merriami. *Animal Behaviour*, 44, pp.1–9.

Dieperink, C., Pedersen, S. and Pedersen, M.I., 2001. Estuarine predation on radiotagged wild and domesticated sea trout (Salmo trutta L.) smolts. *Ecology of Freshwater Fish*, 10, pp.177–183.

Doyle, B.C., Eyto, E. de, Dillane, M., Poole, R., Mccarthy, V. and Jennings, E., 2019. Synchrony in catchment stream colour levels is driven by both local and regional climate. *Biogeosciences*, 16(5), pp.1053–1071.

Esbérard, C.E.L. and Vrcibradic, D., 2007. Snakes preying on bats: New records from Brazil and a review of recorded cases in the Neotropical Region. *Revista Brasileira de Zoologia*, 24(3), pp.848–853.

Esteve, M., 2005. Observations of spawning behaviour in Salmoninae: Salmo, Oncorhynchus and Salvelinus. *Reviews in Fish Biology and Fisheries*, 15(1–2), pp.1–21.

Evans, D., 1994. Observations on the spawning behaviour of male and female adult sea trout, Salmo trutta L., using radio-telemetry. *Fisheries Management and Ecology*, 1, pp.91–105.

Fairman, J.G., Schultz, D.M., Kirshbaum, D.J., Gray, S.L. and Barrett, A.I., 2017.

Climatology of size, shape, and intensity of precipitation features over Great Britain and Ireland. *Journal of Hydrometeorology*, 18(6), pp.1595–1615.

Fenkes, M., Shiels, H.A., Fitzpatrick, J.L. and Nudds, R.L., 2016. The potential impacts of migratory difficulty, including warmer waters and altered flow conditions, on the reproductive success of salmonid fishes. *Comparative Biochemistry and Physiology -Part A : Molecular and Integrative Physiology*, 193, pp.11–21.

Ferguson, A., Reed, T.E., Cross, T.F., McGinnity, P. and Prodöhl, P.A., 2019. Anadromy, potamodromy and residency in brown trout Salmo trutta : the role of genes and the environment. *Journal of Fish Biology*, 95(3), pp.692–718.

Finlay, R., Poole, R., Coughlan, J., Phillips, K.P., Prodöhl, P., Cotter, D., Mcginnity, P. and Reed, T.E., 2020. Telemetry and genetics reveal asymmetric dispersal of a lake-feeding salmonid between inflow and outflow spawning streams at a microgeographic scale. *Ecology and Evolution*, 10(4), pp.1762–1783.

Flávio, H., Kennedy, R., Ensing, D., Jepsen, N. and Aarestrup, K., 2019. Marine mortality in the river ? Atlantic salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment. *Fisheries Management and Ecology*, 27(1), pp.1-92–101.

Fleming, I.A., 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Fish Biology and Fisheries*, 16(6), pp.379–416.

Foster, D.L., Ebling, F.J.P. and Claypool, L.E., 1988. Timing of puberty by photoperiod. *Reproduction Nutrition Development*, 28(2), pp.349–364.

Fraser, N.H.C., Heggenes, J., Metcalfe, N. and Thorpe, J.E., 1995. Low summer

temperatures cause juvenile Atlantic salmon to become nocturnal. *Canadian Journal of Zoology*, 73, pp.446–451.

Fraser, N.H.C. and Metcalfe, N.B., 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic Salmon. *Functional Ecology*, 11, pp.385–391.

García-Vega, A., Sanz-Ronda, F.J. and Fuentes-Pérez, F.J., 2017. Seasonal and daily upstream movements of brown trout Salmo trutta in an Iberian regulated river. *Knowledge and Management of Aquatic Ecosystems*, 418(9), pp.1–9.

Gauthey, Z., Lang, M., Elosegi, A., Tentelier, C., Rives, J. and Labonne, J., 2015. Brown trout spawning habitat selection and its effects on egg survival. *Ecology of Freshwater Fish*, 26, pp.133–140.

Gwinner, E., 1989. Photoperiod as a modifying and limiting factor in the expression of avian circannual rhythms. *Journal of Biological Rhythms*, 4(2), pp.237–250.

Hamilton, R.J. and Kama, W., 2004. *Spawning Aggregations of Coral Reef Fish in Roviana Lagoon , Western Province , Solomon Islands : Local Knowledge Field Survey Report Unrestricted Access Version*. Brisbane.

Hammerschlag, N., Meyer, C.G., Grace, M.S., Kessel, S.T., Sutton, T.T., Harvey, E.S., Paris-Limouzy, C., Kerstetter, D.W. and Cooke, S.J., 2017. Shining a Light on Fish at Night: An Overview of Fish and Fisheries in the Dark of Night, and in Deep and Polar Seas. *Bulletin of Marine Science*, 93, pp.1–32.

Handeland, S.O., Imsland, A.K. and Stefansson, S.O., 2008. The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. *Aquaculture*, 283, pp.36–

42.

Hartig, F., 2019. *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)*.

Hellawell, J.M., Leatham, H. and Williams, G.I., 1974. The upstream migratory behaviour of salmonids in the River Frome, Dorset. *Journal of Fish Biology*, 6, pp.729–744.

Ibbotson, A.T., Beaumont, W.R.C., Pinder, A., Welton, S. and Ladle, M., 2006. Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. *Ecology of Freshwater Fish*, 15, pp.544–551.

Jonsson, B., Jonsson, M. and Jonsson, N., 2017. Influences of migration phenology on survival are size dependent in juvenile Atlantic salmon. *Canadian Journal of Zoology*, 95(8), pp.581–587.

Jonsson, B. and Jonsson, N., 2011. *Ecology of Atlantic salmon and brown trout: Habitat as a template for life histories*. Dordrecht: Springer Netherlands.

Jonsson, N., 1991. Influence of water flow, temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research*, 66, pp.20–35.

Jonsson, N. and Jonsson, B., 2002. Migration of anadromous brown trout Salmo trutta in a Norwegian river. *Freshwater Biology*, 47, pp.1391–1401.

Keenan, K., Bradley, C.R., Magee, J.J., Hynes, R.A., Kennedy, R.J., Crozier, W.W., Poole, R., Cross, T.F., Mcginnity, P. and Prodöhl, P.A., 2013. Beaufort trout MicroPlex: A high-throughput multiplex platform comprising 38 informative microsatellite loci for use in resident and anadromous (sea trout) brown trout Salmo trutta genetic studies. *Journal of Fish Biology*, 82(6), pp.1789–1804.

Kennedy, R.J., Rosell, R., Millane, M., Doherty, D. and Allen, M., 2018. Migration and survival of Atlantic salmon Salmo salar smolts in a large natural lake. *Journal of Fish Biology*, 93(1), pp.134–137.

Kotler, B.T., Brown, J.S. and Hasson, O., 1991. Factors Affecting Gerbil Foraging Behavior and Rates of Owl Predation. *Ecology*, 72(6), pp.2249–2260.

Lampart, W., 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology*, 3(1), pp.21–27.

Last, K.S., Hobbs, L., Berge, J., Brierley, A.S., Last, K.S., Hobbs, L., Berge, J., Brierley, A.S. and Cottier, F., 2016. Moonlight Drives Ocean-Scale Mass Vertical Migration of Zooplankton during the Arctic Winter. *Current Biology*, 26(2), pp.244–251.

Lind, J. and Cresswell, W., 2006. Anti-predation behaviour during bird migration ; the benefit of studying multiple behavioural dimensions. *Journal of Ornithology*, 147, pp.310–316.

Lockard, R.B. and Owings, D.H., 1974. Moon-related surface activity of bannertail (Dipomys spectabilis) and fresno (D. nitratoides) kangaroo rats. *Animal Behaviour*, 22, pp.262–273.

Lüdecke, D., 2018. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *Journal of Open Source Software*, 3, p.772.

Lüdecke, D., Makowski, D. and Waggoner, P., 2019. *performance: Assessment of Regression Models Performance*.

McCormick, S.D., 2012. Smolt Physiology and Endocrinology. *Euryhaline Fishes: Fish Physiology*, 32, pp.199–251.

McLennan, D., Rush, E., Mckelvey, S. and Metcalfe, N.B., 2018. Timing of Atlantic salmon Salmo salar smolt migration predicts successful passage through a reservoir. *Journal of Fish Biology*, 92, pp.1651–1656.

McNamara, J.M., Barta, Z., Klaassen, M. and Bauer, S., 2011. Cues and the optimal timing of activities under environmental changes. *Ecology Letters*, 14, pp.1183–1190.

Metcalfe, N.B., Fraser, N.H.C. and Burns, M.D., 1998. State-dependent shifts between nocturnal and diurnal activity in salmon. *Proceedings of the Royal Society B: Biological Sciences*, 265, pp.1503–1507.

Metcalfe, N.B., Valdimarsson, S.K. and Fraser, N.H.C., 1997. Habitat profitability and choice in a sit-and-wait predator: juvenile salmon prefer slower currents on darker nights. *Journal of Animal Ecology*, 66, pp.866–875.

Montgomery, D.R., Beamer, E.M., Pess, G.R. and Quinn, T.P., 1999. Channel type and salmonid spawning distribution and abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(3), pp.377–387.

Moore, A., Bendall, B., Barry, J., Waring, C., Crooks, N. and Crooks, L., 2012. River temperature and adult anadromous Atlantic salmon, Salmo salar, and brown trout, Salmo trutta. *Fisheries Management and Ecology*, 19, pp.518–526.

Morbey, Y., 2000. Protandry in Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, pp.1252–1257.

Morbey, Y.E., 2002. Protandry models and their application to salmon. *Behavioral Ecology*, 13(3), pp.337–343.

Morbey, Y.E. and Ydenberg, R.C., 2001. Protandrous arrival timing to breeding

areas : a review. *Ecology Letters*, 4, pp.663–673.

Morrison, D.W., 1978. Lunar phobia in a neotropical fruit bat, Artibeus jamaicensis (Chiroptera: Phyllostomidae). *Animal Behaviour*, 26, pp.852–855.

Neuheimer, A.B. and Taggart, C.T., 2007. The growing degree-day and fish size-at-age : The overlooked metric. *Canadian Journal of Fisheries and Aquatic Science*, 64, pp.375–385.

Nevoux, M., Finstad, B., Davidsen, J.G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O. and Jonsson, B., 2019. Environmental influences on life history strategies in partially anadromous brown trout (Salmo trutta, Salmonidae). *Fish and Fisheries*, 20(6), pp.1051–1082.

Ohman, M.D., 1990. The Demographic Benefits of Diel Vertical Migration by Zooplankton. *Ecological Monographs*, 60(3), pp.257–281.

Olsson, I.C., Greenberg, L.A. and Eklöv, A.G., 2011. Effect of an Artificial Pond on Migrating Brown Trout Smolts. *North American Journal of Fisheries Management*, 21, pp.498–506.

Ovidio, M., 1999. Annual activity cycle of adult brown trout (Salmo trutta L .): A radio-telemetry study in a small stream of the Belgian Ardenne. *Bulletin Français de la Pêche et de la Pisciculture*, 352, pp.1–18.

Ovidio, M., Baras, E., Goffaux, D., Birtles, C. and Philippart, J.C., 1998. Environmental unpredictability rules the autumn migration of brown trout (Salmo trutta L.) in the Belgian Ardennes. *Hydrobiologia*, 371, pp.263–274.

Ovidio, M., Baras, E., Goffaux, D., Giroux, F. and Philippart, J.C., 2002. Seasonal variation of activity pattern of brown trout (Salmo trutta) in a small stream as

determined by radio-telemetry. *Hydrobiologia*, 470, pp.195–202.

Palmer, S.M., Fieberg, J., Swanson, A., Kosmala, M. and Packer, C., 2017. A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecology Letters*, 20(11), pp.1–10.

Pankhurst, N.W. and King, H.R., 2010. Temperature and salmonid reproduction : implications for aquaculture. *Journal of Fish Biology*, 76, pp.69–85.

Pépino, M., Rodríguez, M.A. and Magnan, P., 2015. Shifts in movement behavior of spawning fish under risk of predation by land-based consumers. *Behavioral Ecology*, 26(4), pp.996–1004.

Piecuch, J., Lojkásek, B., Lusk, S. and Marek, T., 2007. Spawning migration of brown trout, Salmo trutta in the Morávka reservoir. *Folia Zoologica*, 56(2), pp.201–212.

Poole, W.R., Reynolds, D. and Moriarty, C., 1990. Observations on the Silver Eel Migrations of the Burrishoole River System, Ireland, 1959 to 1988. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 75(6), pp.807–815.

Pratas-Santiago, L.P., Gonçalves, A.L.S., Nogueira, A.J.A. and Spironello, W.R., 2017. Dodging the moon: The moon effect on activity allocation of prey in the presence of predators. *Ethology*, 123(6–7), pp.467–474.

Prentice, E.F., Flagg, T.A. and McCutcheon, C.S., 1990. Feasibility of Using Implantable Passive Integrated Transponder (PIT) Tags in Salmonids. *American Fisheries Society Symposium*, 7, pp.317–322.

Quinn, T.P. and Buck, G.B., 2001. Size- and Sex-Selective Mortality of Adult Sockeye Salmon: Bears, Gulls, and Fish Out of Water. *Transactions of the American*

Fisheries Society, 130(6), pp.995–1005.

Quinn, T.P., Unwin, M.J. and Kinnison, M.T., 2000. Evolution of temporal isolation in the wild: Genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution*, 54(4), pp.1372–1385.

R_Core_Team, 2019. *R: A Language and Environment for Statistical Computing*.

Rappole, J.H., 2013. *The Avian Migrant: The Biology of Bird Migration*. 1st ed. New York: Columbia University Press.

Remisiewicz, M. and Wennerberg, L., 2006. Differential migration strategies of the Wood Sandpiper (Tringa glareola) - Genetic analyses reveal sex differences in morphology and spring migration phenology. *Ornis Fennica*, 83(1), pp.1–10.

Robart, A.R., McGuire, M.M.K. and Watts, H.E., 2018. Increasing photoperiod stimulates the initiation of spring migratory behaviour and physiology in a facultative migrant , the pine siskin. *Royal Society Open Science*, 5(8), pp.1–12.

Robinson, F.W. and Tash, J.C., 1979. Feeding by Arizona trout (Salmo apache) and brown trout (Salmo trutta) at different light intensities. *Environmental Biology of Fishes*, 4(4), pp.363–368.

Rustadbakken, A., L'Abee-Lund, J.H., Arnekleiv, J.V., Kraabøl, M., L'Abée-Lund, J.H., Arnekleiv, J.V. and Kraabøl, M., 2004. Reproductive migration of brown trout in a small Norwegian river studied by telemetry. *Journal of Fish Biology*, 64, pp.2–15.

Sandlund, O.T., Diserud, O.H., Poole, R., Bergesen, K., Dillane, M., Rogan, G., Durif, C., Thorstad, E.B. and Vøllestad, L.A., 2017. Timing and pattern of annual silver eel migration in two European watersheds are determined by similar cues.

Ecology and Evolution, 7(15), pp.5956–5966.

Santos, J.M., Ferreira, M.T., Godinho, F.N. and Bochechas, J., 2002. Performance of fish lift recently built at the Touvedo Dam on the Lima River, Portugal. *Journal of Applied Ichthyology*, 18, pp.118–123.

Schwinn, M., Aarestrup, K., Baktoft, H. and Koed, A., 2017. Survival of Migrating Sea Trout (Salmo trutta) Smolts During Their Passage of an Artificial Lake in a Danish Lowland Stream. *River Research and Applications*, 33(4), pp.558–566.

Seamons, T.R., Bentzen, P. and Quinn, T.P., 2004. The mating system of steelhead, Oncorhynchus mykiss, inferred by molecular analysis of parents and progeny. *Environmental Biology of Fishes*, 69, pp.333–344.

Serbezov, D., Bernatchez, L., Olsen, E.M. and Vollestad, L.A., 2010. Mating patterns and determinants of individual reproductive success in brown trout (Salmo trutta) revealed by parentage analysis of an entire stream living population. *Molecular Ecology*, 19, pp.3193–3205.

Slavík, O., Horký, P., Maciak, M., Horka, P. and Langrová, I., 2018. Diel movement of brown trout, Salmo trutta, is reduced in dense populations with high site fidelity. *Ecology and Evolution*, 8(9), pp.4495–4507.

Slavík, O., Horký, P., Randák, T., Balvín, P. and Bílý, M., 2012. Brown Trout Spawning Migration in Fragmented Central European Headwaters : Effect of Isolation by Artificial Obstacles and the Moon Phase. *Transactions of the American Fisheries Society*, 141, pp.673–680.

Šmejkal, M., Souza, A.T., Blabolil, P., Bartoň, D., Sajdlová, Z., Vejřík, L. and Kubečka, J., 2018. Nocturnal spawning as a way to avoid egg exposure to diurnal

predators. *Nature- Scientific Reports*, 8(1), pp.1–7.

Tappel, P.D. and Bjornn, T.C., 1983. A New Method of Relating Size of Spawning Gravel to Salmonid Embryo Survival. *North American Journal of Fisheries Management*, 3(2), pp.123–135.

Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H. and Finstad, B., 2012. A critical life stage of the Atlantic salmon Salmo salar: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81(2), pp.500–542.

Tøttrup, A.P. and Thorup, K., 2008. Sex-differentiated migration patterns, protandry and phenology in North European songbird populations. *Journal of Ornithology*, 149(2), pp.161–167.

Visser, M.E. and Both, C., 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, 272, pp.2561–2569.

Walton, J.C., Weil, Z.M. and Nelson, R.J., 2011. Influence of photoperiod on hormones, behavior, and immune function. *Neuroendocrinol*, 32(3), pp.303–319.

Werner, E.E. and Gilliam, J.., 1984. The Ontogenetic Niche and Species Interactions in Size-Structured Populations. *Annual Review of Ecology and Systematics*, 15(1), pp.393–425.

Whelan, C.L. and Wyneken, J., 2007. Estimating Predation Levels and Site-Specific Survival of Hatchling Loggerhead Seaturtles (Caretta caretta) from South Florida Beaches. *American Society of Ichthyologists and Herpetologists*, 3, pp.745–754.

Whelan, K.F., Poole, W.R., McGinnity, P., Rogan, G. and Cotter, D., 1998. The

Burrishoole System. In: *Studies of Irish Rivers and Lakes, Essays on the occasion of the XXVII Congress of Societas Internationalis Limnologiae (SIL)*. Dublin.pp.191–212.

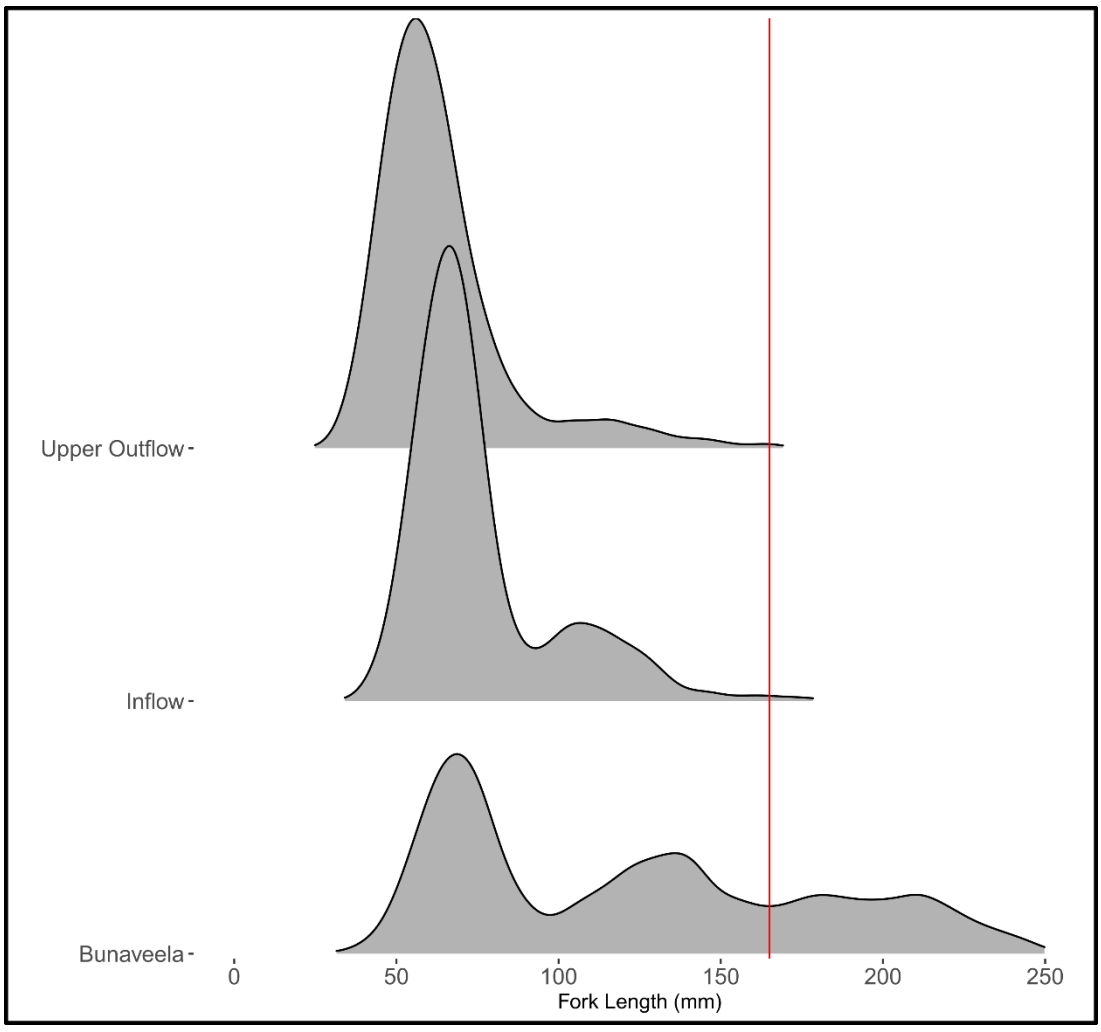
Zavorka, L., Aldven, D., Naslund, J., Hojesjo, J. and Jonsson, J.I., 2016. Inactive trout come out at night: behavioral variation, circadian activity, and fitness in the wild. *Ecology*, 97(9), pp.2223–2231.

Zehnder, S., Akesson, S., Liechti, F. and Bruderer, B., 2001. Nocturnal autumn bird migration at Falsterbo, South Sweden. *Journal of Avian Biology*, 3, pp.239–248.

Supporting information

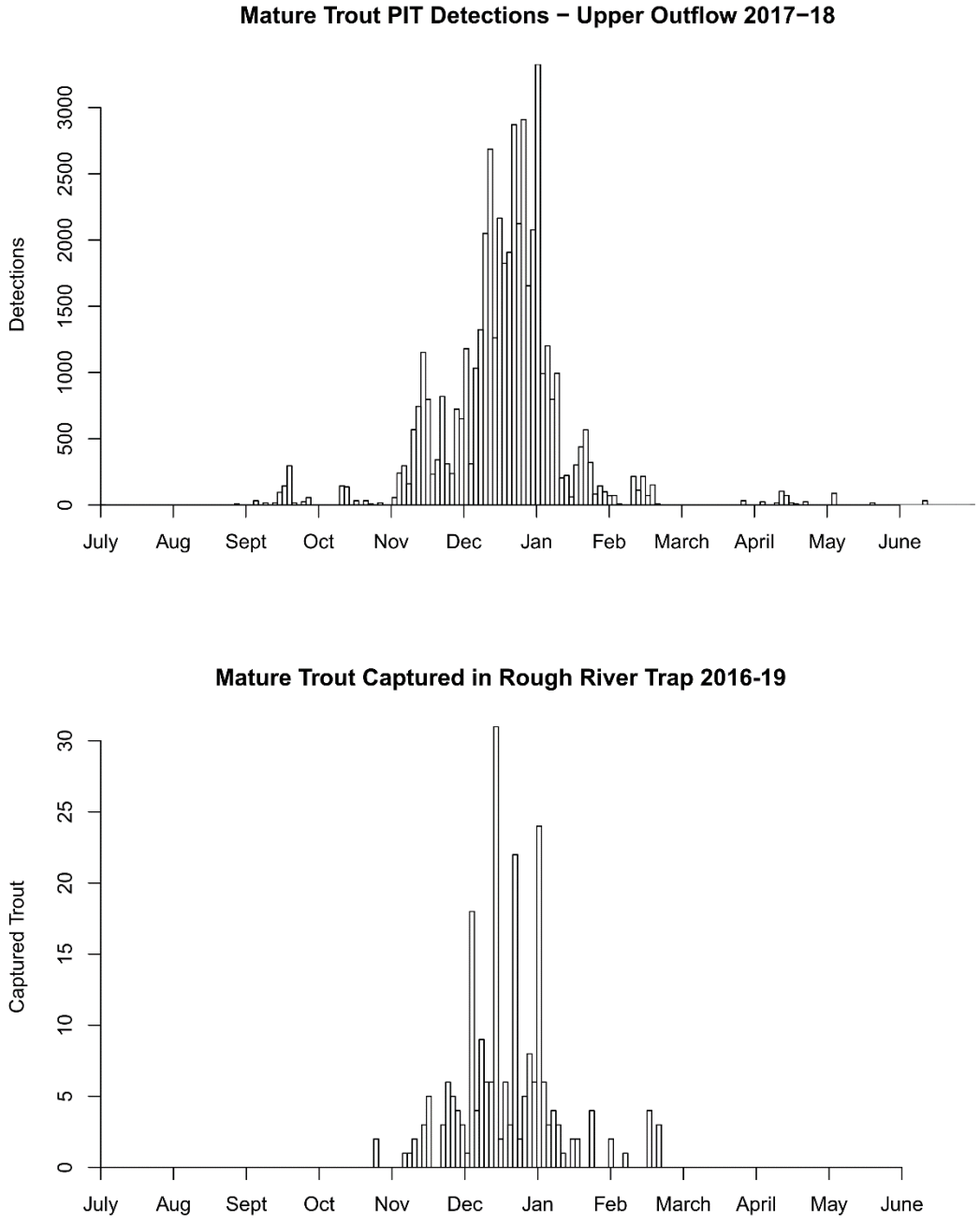
3675

Spawning-related movements in a salmonid appear timed to reduce exposure to visually-oriented predators



3680

Figure S1. Size distribution (FL) of trout sampled from June to September in the upper outflow (N = 1,136) and the inflow (N = 877) between 2005 and 2017, and from Bunaveela Lough (N = 3,176) between 1991 and 2017. The red line at 165 mm represents the threshold length for maturity selected for this study (~mean – 1 SD).



3685

Figure S2. Mature-sized trout detected at the upper outflow antennae (July 2017 to June 2018) and trout identified as mature (either ripe or spent) in the Rough River fish trap (2016-2019).

3690

Table S1: Hydrological properties of Bunaveela Lough, the upper outflow and the inflow streams.

Site	pH	Conductivity µS cm-1	Alkalinity ($CaCO_3$ equiv. mg/l)	Nitrogen (mg/l)	Phosphorous (µg/l)
Bunaveela	7.2	86	33.0	0.657	17.66
Inflow	7.23	116	30.87	0.274	15
Upper Outflow	7.05	96.65	10.14	0.238	7

Table S2. Summary of trout that were caught, tagged or recaptured in Bunaveela Lough, Lough Feeagh and the Rough River traps during the project.

Date	**Site**	**# of Seine Net Hauls**	**Trout Tagged FL>70 mm**	**Trout FL<70 mm**	**Trout Recaptured (previously tagged)**
11/10/2016	Bunaveela	5	44	0	0
21/06/2017	Bunaveela	5	147	13	1
23/06/2017	Feeagh	5	71	0	4
16/08/2017	Bunaveela	6	102	16	14
21/08/2017	Feeagh	6	52	0	17
26/10/2017	Bunaveela	6	91	6	19
27/10/2017	Feeagh	6	31	0	12
24/10/2018	Bunaveela	4	41	6	10
08/11/2018	Bunaveela	3	31	3	10
Daily	Rough River Traps	NA	1759	165	287
	Total	NA	2369	209	374

3695

Table S3. Proportion of mature-sized trout caught in the Rough River fish trap per month that were visually identified as 'ripe' (i.e. ready to breed), 'not yet ripe' (i.e. not displaying any physical characteristics indicative of sexual maturity) and 'spent' (i.e. have finished spawning). 2017-2019.

	N	Not Yet Ripe	Ripe	Spent
Oct	16	0.750	0.250	0.000
Nov	66	0.182	0.621	0.197
Dec	86	0.047	0.267	0.686
Jan	67	0.075	0.050	0.875
Feb	6	0.000	0.000	1.000

Telemetry and genetics reveal asymmetric dispersal of lake-feeding salmonid between inflow and outflow spawning streams at a microgeographic scale

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Key Words: Sympatric populations; Lake; Dispersal; Philopatry; Local adaptation; Telemetry.

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Abstract

The degree of natal philopatry relative to natal dispersal in animal populations has important demographic and genetic consequences and often varies substantially within species. In salmonid fishes, lakes have been shown to have a strong influence on dispersal and gene flow within catchments; for example, populations spawning in inflow streams are often reproductively isolated and genetically distinct from those spawning in relatively distant outflow streams. Less is known, however, regarding the level of philopatry and genetic differentiation occurring at microgeographic scales, e.g. where inflow and outflow streams are separated by very small expanses of lake habitat. Here we investigated the interplay between genetic differentiation and fine-scale spawning movements of brown trout between their lake-feeding habitat and two spawning streams (one inflow, one outflow, separated by < 100 m of lake habitat). Most (69.2%) of the lake-tagged trout subsequently detected during the spawning period were recorded in just one of the two streams, consistent with natal fidelity, while the remainder were detected in both streams, creating an opportunity for these individuals to spawn in both natal and non-natal streams. The latter behaviour was supported by genetic sibship analysis, which revealed several half-sibling dyads containing one individual that was sampled as a fry in the outflow and another that was sampled as fry in the inflow. Genetic clustering analyses in conjunction with telemetry data suggested that asymmetrical dispersal patterns were occurring, with natal fidelity being more common amongst individuals originating from the outflow than the inflow stream. This was corroborated by Bayesian analysis of gene flow, which indicated significantly higher rates of gene flow from the inflow into the outflow than vice versa. Collectively, these results reveal how a combination of telemetry and genetics can identify distinct reproductive behaviours and

associated asymmetries in natal dispersal that produce subtle, but nonetheless biologically relevant, population structuring at microgeographic scales.

Introduction

Natal philopatry, whereby individuals return to their birth place for reproduction, limits gene flow between geographic areas and thereby increases neutral genotypic differentiation among populations via genetic drift. When ecological conditions vary across space, natal philopatry can also facilitate the evolution of local adaptation (Kawecki and Ebert, 2004), which in turn influences the resilience of metapopulations and species in the face of environmental change (Hilborn et al., 2003; Schindler, Armstrong and Reed, 2015). However, the geographic scales over which local adaptation operates within salmonid species remains poorly characterised (Adkison, 1995; Fraser et al., 2011). In contrast to philopatry, natal dispersal promotes gene flow, increasing genetic diversity and thus reducing the likelihood of inbreeding within populations and homogenising genetic structure among populations, sometimes at the expense of local adaptation (Garant, Forde and Hendry, 2007). Rates of philopatry versus dispersal can vary within a single species with respect to sex, age, life history or environmental factors (De Fraipont et al., 2000; Förschler, del Val and Bairlein, 2010; Purdue, Smith and Patton, 2000; Winkler et al., 2006; Lesage et al., 2000). At the individual level, these behaviours are associated with a range of context-dependent fitness consequences, with many theories having been proposed for when selection should favour philopatry over dispersal, or vice versa (see review by Hendry et al., 2004).

Dispersal is distinct from migration, in a behavioural sense, with the latter corresponding to spatially and temporally predictable movement of individuals

among breeding and foraging or refuge habitats (Dingle and Drake, 2007). However, dispersal and migration can be related. For example, resident passerine birds exhibit higher rates of natal philopatry (i.e. reduced natal dispersal) relative to migratory passerine birds (Weatherhead and Forbes, 1994). Similarly, genetic differentiation appears to be greater among lake- and stream-resident populations of brown trout (*Salmo trutta*) compared to anadromous (sea-migrating) populations (Östergren and Nilsson, 2012), implying that 'straying' (i.e. natal dispersal) rates may be higher in the latter, perhaps due to constraints on homing abilities.

Brown trout in general exhibit a broad range of migratory strategies and distances (Ferguson et al., 2019; Nevoux et al., 2019), making them a particularly interesting species for studying links between movement behaviour, dispersal versus philopatry, and the extent of demographic and genetic connectedness of populations. Natal philopatry in salmonids involves a complex interaction between evolved genetic mechanisms and proximal responses to environmental and social cues (Dittman and Quinn, 1996). Together these mechanisms allow salmonids to 'home' back to their natal river and even the natal sites from which they originated, despite intervening movements or feeding migrations that can range in extent from tens of meters to thousands of kilometres (Neville et al., 2006; Stewart, Quinn and Bentzen, 2003; Quinn, Stewart and Boatright, 2006). The geographic scale and consistency at which such homing behaviour operates remains uncertain, although individual Atlantic salmon have been recorded breeding in multiple redds separated by distances ranging from less than five meters up to more than five kilometres (Taggart et al., 2001). Juvenile salmonids imprint on (i.e. learn) the odours of their natal stream prior to, or during, out-migration from it (Dittman and Quinn, 1996; Keefer and Caudill, 2014). However, interrupted or imperfect imprinting during rearing or

juvenile migration can increase straying rates (Keefer and Caudill, 2014). There also appear to be genetically-based differences across populations in straying rates and distances (King et al., 2016; Keefer and Caudill, 2014; Jonsson and Jonsson, 2014, 2017), with selection thought to favour higher straying when habitat quality or quantity fluctuates unpredictably through time (Quinn and Tallman, 1987; Hendry et al., 2004).

In addition to behavioural and life history characteristics, landscape or seascape features also play a strong role in promoting or limiting dispersal and thus shaping patterns of intraspecific genetic diversity across space. For example, population structure in freshwater fishes tends to greatly exceed that found in marine fishes, perhaps due to the presence of more physical barriers to dispersal within and amongst freshwater systems (Tonteri et al., 2007; Ward, Woodwark and Skibinski, 1994). Waterfalls, culverts, dams and other landscape features can obstruct movement within river systems in both directions or in just one, with the latter situation providing a mechanism for asymmetric dispersal and gene flow (Prodőhl et al., 2019; Torterotot et al., 2014). Asymmetric dispersal, which also occurs in terrestrial habitats where it is often wind-driven (Sanmartı, Wanntorp and Winkworth, 2007; Cook and Crisp, 2005), and in marine environments where it is often driven by ocean currents (Storch and Pringle, 2018; Pringle et al., 2011), can effectively generate a source-pseudosink population structure (sensu Watkinson and Sutherland, 1995) in which natural selection should be biased in favour of the source ('upstream') habitat (Kawecki and Holt, 2002). Additionally, river characteristics can interact with homing and life-history differences to influence the genetic diversity and structure of salmonid populations (Vähä et al., 2007; Gomez-Uchida, Knight and Ruzzante, 2009; Ozerov et al., 2012; Bradbury et al., 2013; Mcphee et

al., 2014), as may the presence of lakes within watersheds (Dillane et al., 2008; Jacobs et al., 2018; Massa-Gallucci et al., 2010; McKeown et al., 2010; Palmé, Laikre and Ryman, 2013). In addition to isolation by dispersal limitation, so-called 'isolation by adaptation' processes may serve to increase genome-wide differentiation among populations, where natural selection plays an indirect role by reducing gene flow among ecologically divergent habitats, owing to reduced fitness of immigrants (Nosil, Egan and Funk, 2008; Orsini et al., 2013). With reduced gene flow, populations are 'free' to diverge under the influence of random genetic drift. Isolation by adaptation has been invoked to explain spatial patterns of genetic diversity in salmonids linked with, for example, climate (Dionne et al., 2008; Olsen et al., 2011; Hand et al., 2016), geological substrate (Perrier et al., 2011), pathogens (de Eyto et al., 2011) and metal contamination (Paris, King and Stevens, 2015).

In this study, we use a combination of telemetry and genetics to investigate the interplay between putative homing/straying behaviours and genetic differentiation among spawning streams at a micro-geographic scale (*sensu* Richardson et al., 2014) in non-anadromous brown trout. The species typically exhibits hierarchical population genetic structure across a range of spatial scales (Lobón-Cerviá and Sanz, 2017), sometimes down to scales of < 1 km (Carlsson et al., 1999), implying either low straying rates at these micro-geographic scales, or fine-scale local adaptation that constrains gene flow if straying does occur. Brown trout often exploit lakes for growing and rearing, which can involve short- or long-distance migrations between natal streams and lacustrine habitat. A particularly interesting scenario arises where brown trout spawn in both inflowing and outflowing streams, but co-occur in a more productive lake habitat for much of their lives. Juveniles spawned in lake-outflows must conduct upstream feeding migrations

to reach lake habitat, actively swimming against the flow of the river. Such upstream feeding migrations would presumably be maladaptive in lake-inflow streams, as this behaviour would move juveniles away from, rather than towards, the lake, where growth opportunities are higher. Thus, inflowing and outflowing streams may exert differing selective pressures by virtue of their flow direction, which in turn could promote genome-wide genetic divergence via the above mechanisms. Indeed, Jonsson et al. (1994) demonstrated that the offspring of inflow and outflow spawning brown trout displayed different directional migratory responses to water current, a population-specific juvenile rheotactic response pattern that has been identified in various salmonid species (Kelso and Northcote, 1981; Bowler, 1975; Brannon, 1972; Kaya, 1991; Raleigh, 1967; Raleigh and Chapman, 1971; Raleigh, 1971). Additionally, brown trout populations that utilise common lake feeding habitat but are genetically, behaviourally and morphologically distinct have been found to display reproductive isolation by homing back to separate inflow or outflow rivers for spawning (Ferguson and Taggart, 1991; Ferguson and Mason, 1981; Jacobs et al., 2018). Reproductive isolation appears to promote similar differentiation amongst sympatric lake-dwelling populations of rainbow smelt (*Osmerus mordax*) (Taylors and Bentzent, 1993), Arctic charr (*Salvelinus alpinus* L.) (Jonsson and Jonsson, 2001), Dolly Varden (*Salvelinus malma*) (Markevich, Esin and Anisimova, 2018), and sockeye salmon (*Oncorhynchus Nerka*) (Moreira and Taylor, 2015). It remains unknown, however, whether consistent, accurate homing behaviour and associated genetic divergence occurs between lake inflow and lake outflow streams at microgeographic scales of less than 100 m.

Here we investigated these issues in a small lake in the west of Ireland fed and drained respectively by a single inflowing and a single outflowing stream,

separated by less than a hundred meters of lake habitat. We hypothesised that a combination of pre- and post-zygotic isolating mechanisms should have produced weak to moderate neutral genetic differentiation between brown trout originating in the inflow and outflow streams, and that gene flow patterns between these groups may not be symmetrical. As our first aim, we used PIT-tag telemetry to monitor lake-to-stream movements of spawning-sized fish to determine whether some fish exhibited behaviour consistent with philopatry (only detected in one of the streams) while the behaviour of others was consistent with straying (detected in both streams). A fish detected during the spawning season in only one of the streams may, of course, have been born in the other and thus have been exhibiting straying behaviour. In the absence of more direct methods for detecting homing versus straying, genetic techniques can be used to assign fish sampled as adults in the lake to population genetic clusters that may correspond to inflow versus outflow spawning streams if gene flow is restricted. Similarly, parental movements may be inferred indirectly using genetic sibship analysis: if fry sampled in both streams assign to the same half-sib group, for example, this suggests that one of their parents spawned in both streams. Our second aim was therefore to use a range of genetic analyses, including clustering approaches, to identify any such half-sibships, test for fine-scale population structure, characterise patterns of gene flow between the streams (symmetric versus asymmetric) and interpret these patterns in light of the behavioural data and vice versa.

Materials and methods

Study area

The Burrishoole catchment in the north west of Ireland is a complex freshwater system comprised of three main lakes linked by a network of rivers and streams that drain an area of approximately 83 km^2. Bunaveela Lough (54º 01' 18" N 9º 32' 43" W), the most northerly and the most elevated of the three lakes, has a surface area of 46 ha, a maximum depth of 23 m, and supports populations of brown trout (*Salmo trutta* L.), Atlantic salmon (*Salmo salar* L.), Arctic char (*Salvelinus alpinus* L.) and European eel (*Anguilla anguilla* L.). Seine netting surveys indicate that trout are relatively abundant in the lake, outnumbering salmon and char within the littoral zone by more than five to one. The lake is fed by a single inflowing stream, the Fiddaunveela, and drained by a single outflowing stream, the Goulaun. The straight-line distance between the point at which the Fiddaunveela flows into the lake and the point at which the Goulaun flows out of the lake is 98 m. The inflow is a shallow and flood-prone stream of approximately 2010 m in length, draining a steep valley to the south east of the lake. The outflow flows south west from Bunaveela Lough for 10,345 m before entering Lough Feeagh (410 ha), increasing significantly in size as it approaches Feeagh. Due to the regulating effect of Bunaveela, the upper stretches of the outflow are less prone to rapid fluctuations in flow rates than the inflow. Although pH during baseflow is circumneutral in the two streams, they are both small, poorly buffered and oligotrophic, and therefore offer limited feeding and growth opportunities to resident trout (hydrological conditions described in Supporting Information, Table S1). In contrast, much of Bunaveela Lough is comparatively well buffered and productive due to limestone and sandstone deposits

(Whelan et al., 1998) and consequently the lake represents an alternative feeding habitat where growth may be less constrained (trout size distributions in streams and lake shown in Supporting Information, Fig. S1).

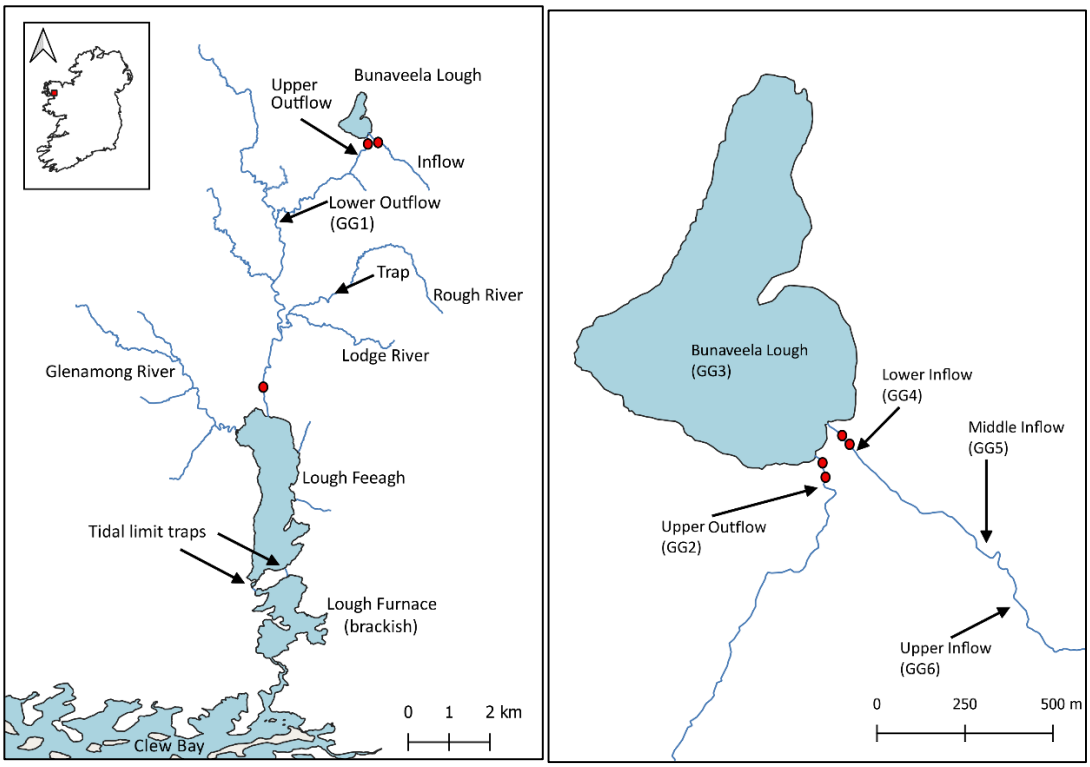


Figure 1. Map of the Burrishoole catchment, Co. Mayo, Ireland. Red circles are locations of PIT antennae. GG refers to geographic groups, i.e. sites where groups of fish were sampled.

Sampling

Trout fry and parr were captured during the summers of 2017 and 2018 by electrofishing (electrofisher model: Hans Grassl IG600) in the upper and lower sections of the outflow (n = 181) and the upper, middle and lower sections of the inflow (n = 208) (Fig. 1). A total of 500 additional trout (fry, parr and adults) were captured from the south eastern shore of Bunaveela Lough (henceforth 'Bunaveela')

by seine netting (9 mm mesh) across six dates between October 2016 and October 2018 (details in Supporting Information, Table S2). All trout were anaesthetised in pH-buffered tricaine methane sulphonate (80 mg l^{-1}), measured (fork length, FL, mm), weighed (to 0.1 g) and a small clip (approx. 2 mm^2) was taken from the caudal fin and stored in 95% ethanol for genetic analysis. Each trout of > 70 mm (n = 605) was implanted with a uniquely coded 12 mm half-duplex (HDX) passive integrated transponder (PIT) tag (Biomark 134.2 kHz ISO HDX). PIT tags were implanted into the peritoneal body cavity through a needle inserted just posterior to the tip of the pectoral fin and to one side of the mid-ventral line at the tips of the pleural ribs. After sampling, anaesthetised fish were moved to a tank of aerated fresh river or lake water and monitored until their equilibrium was fully regained and active swimming recommenced. Once recovered, all fish were released back into the site from which they were originally captured. PIT tagging and fin clipping were carried out in accordance with S.I. No.123/2014 Animal Health and Welfare (operations and procedures) Regulations 2014 and with approval of the MI animal welfare committee.

In order to characterise movement patterns at a broader catchment scale and thus contextualise any fine-scale genetic structure observed during subsequent analysis, a combination of electrofishing and seine netting was used to capture trout of a range of sizes in Lough Feeagh and three of its tributaries (the Rough River, the Lodge River and the Glenamong River) (Fig. 1) over 32 dates between October 2016 and October 2018 (Supporting Information, Table S2). Additionally, between December 2016 and March 2019 one fish trap was operated continuously in the Rough River (RR), a river that is utilised by lake feeding trout for spawning, and two other traps were operated at tidal limit of the river system. Trout that had been actively captured

or trapped in either of the above cases were measured, visually assessed for maturity status, scanned for PIT tags, and all untagged individuals > 70 mm (n = 3617) were PIT tagged. A length distribution for trout confirmed as mature (i.e. displaying physical characteristics indicative of imminent or recent mating) was generated and used to designate a minimum threshold 'mature' length (mean FL minus 1 SD of mature fish) for use in behavioural analyses. A conservative threshold of one standard deviation below the mean was used here in order to maximise the chances of only including true mature fish in the telemetry analyses (as we were interested in spawning movement behaviours specifically), i.e. to exclude larger immature fish that may have been similar in size to relatively small mature fish.

Most of the trout that were PIT-tagged in Bunaveela (87.6%) were only caught once (up to 811 days prior to the spawning period during which they were detected on an antenna), and therefore their actual size at spawning time was unknown. To estimate this, and thereby exclude any individuals that were below our threshold mature length from subsequent analyses, we used FL data from 87 PIT tagged lake-feeding trout that were recaptured during the study period (from 15 to 505 days after tagging) to calibrate a linear model to describe growth per degree day in the statistical program R v3.5.2 (R_Core_Team, 2019). This then allowed us to infer the likely growth (from tagging to spawning period) of fish that were only measured at tagging, giving an estimate of their FL during the spawning period. Previous studies have shown that individual growth rate within fish populations is largely a function of temperature and individual size (Neuheimer and Taggart, 2007; Handeland, Imsland and Stefansson, 2008; Boltaña et al., 2017). Throughout the study period, high frequency lake surface temperature data were recorded in Lough Feeagh (~7 km SW of Bunaveela) (de Eyto et al., 2019) and, due to the physical similarities and

geographical proximity of the lakes, these temperatures were used as a proxy for Bunaveela surface water temperatures. By including a base temperature (T_0), calculations were limited to temperatures relevant to growth, or 'growing degree days' (GDD) (Chezik, Lester and Venturelli, 2014). FL at tagging date and GDD between tagging date and recapture date were treated as explanatory variables while growth over the same period was treated as the response variable in the model. The best value for T_0, in statistical terms, was determined by maximising model R^2 value from a range of base temperatures (0°C-12°C inclusive). The model containing the optimised T_0 was then used to estimate individual growth since tagging (and thus final FL) as a function of initial FL and intervening GDD.

Monitoring behaviour –PIT telemetry

In order to investigate the movement of lake-feeding trout during the spawning season, as well as the degree of movement between the upper and lower Burrishoole catchment, a network of five swim-through, cross-channel HDX PIT antennae powered by Oregon RFID multiplexing readers was installed between August and September 2017 and maintained for the duration of the study period. HDX PIT antennae generate an electromagnetic field that wirelessly powers any nearby HDX PIT tag, causing the tag to transmit a unique 12-digit identification number that is subsequently received and recorded by the antenna reader along with the date and time. The scan rates of all readers were set to ten transmit-receive cycles s^{-1}. Two antennae were installed in the lower inflow, 75 m and 85 m upstream of Bunaveela, and two antennae were installed in the upper outflow, 40 m and 60 m downstream of the lake (Fig.1). A single antenna was installed in the lower outflow, 9,540 m downstream from Bunaveela and 805 m upstream from Lough Feeagh (Fig.1). Each

antenna was designed to span the entire channel width and depth at its location during all but exceptionally high flow conditions. The performance of each antenna was checked with a test tag every 10 to 14 days and shortly after each flood event. When required, repairs were generally completed within 48 hours of antenna damage in order to ensure that antennae remained operational throughout the vast majority study period.

A combination of daily data on the maturity status of trout moving upstream and downstream through the RR fish traps and PIT-derived behavioural data for Bunaveela-tagged trout deemed mature was used to designate a spawning migration period for Burrishoole trout, running from the 1st of November to the 28th of February. Annual movements of mature-sized lake-tagged trout past the fluvial antennae occurred almost exclusively during this period (see results and Supporting Information, Fig. S2), suggesting that movements recorded at this time of the year were primarily motivated by reproduction rather than exploratory foraging. For the purpose of characterising discrete behavioural tactics, mature trout detected only on the inflow antennae were categorised simply as 'inflow-only' (IO) fish, and mature fish detected only on the upper outflow antennae as 'outflow-only' (OO) fish. Fish from each of these categories could be exhibiting homing behaviour to their natal streams, or straying behaviour if born in the other stream - the telemetry data alone cannot distinguish these, but genetic inference may facilitate such distinctions (see below). Mature trout detected on antennas in both streams during the spawning window were categorised simply as B fish (standing for 'both'), which could be exhibiting either homing or straying, or both; clearly they moved from the lake to both streams, but they may not have spawned in them.

Genetics

DNA extraction

Genomic DNA was extracted from caudal tissue from 853 samples using the Promega Wizard® SV 96 Genomic DNA Purification System. DNA quality and quantity was assessed on agarose gels by comparison with a Quick-Load® Purple 100 bp DNA Ladder (New England Biolabs). Concentration of DNA for PCR was adjusted to 2-10ng/µl

PCR

Multiplex PCR (two independent reactions) was used to amplify 18 microsatellite loci (1- Ssa197; 2- Ssa85; 3- SsaD71; 4- Ssa410UOS; 5- Ssa416; 6- CAO48828; 7- CAO53293; 8- CAO60177; 9- BG935488; 10- One102-a; 11- One102-b; 12- One103; 13- One108; 14- ppStr3; 15- Cocl-lav-4; 16- SasaTAP2A; 17- MHC-I; 18- One9Asc) in addition to one sex marker, which was developed from the SalmoYF sequence available in GeneBank (P. Prodöhl, unpublished). These microsatellites, selected from a panel comprising 38 markers characterised and optimised by Keenan et al. (2013) for *Salmo trutta* genetic research, had been found to be very reliable, consistent and informative for population genetic structuring (Prodöhl et al. 2017). All PCRs were performed in 3.5µl volume, including ~2-10ng of genomic DNA and 1.75µl Plain Combi PPP Master Mix (TopBio). Further primer details (e.g. original references, fluorescent label employed, concentrations) and PCR cycling parameters are given in Keenan et al. (2013). Amplified fragments were resolved on either a 24 capillary ABI3500xL (University College Cork) or a 96 capillary ABI3730XL (Queens University Belfast) DNA analysers using POP-7™ polymer and GeneScan™ 600 LIZ™ dye as size standard (ThermoFisher Scientific). Genotyping

(allele calling) was executed using GeneMarker (SoftGenetics). The genetic sex of each individual was determined based on the presence or absence of an amplified DNA fragment of 108 base pairs at the locus SalmoYF. This fragment is present in male brown trout but not in females.

Tests for genotyping errors

All loci were tested for the presence of genotyping errors due to null alleles or large allele dropout using MICRO-CHECKER v2.2.3 (Van Oosterhout et al., 2004). Four loci, BG935488, Ssa85, CAO53293 and MHC-I showed evidence of high frequencies (8-12%) of null alleles. Additionally, GENEPOP v4.2 (Rousset, 2008) was used to test each locus in each sampling group for Hardy-Weinberg equilibrium (HWE). F_{IS} for these four loci was > 0.15 in at least six out of eleven sampling groups, indicating strong heterozygote deficiencies. No other locus exhibited evidence of strong or frequent heterozygote deficiency and, as a result, the four loci identified by MICRO-CHECKER were excluded from all subsequent analyses. The revised 14 loci dataset was checked for unscored alleles and any individual with fewer than 10 scored loci was removed from downstream analyses (n = 9), leaving 844 successfully genotyped samples.

Parentage and sibship analysis

In order to control for the influence of full-sibling groups on genetic structure analyses and identify mixed-site half-sibling groups (i.e. half-sibs sampled in different places) that could be indicative of non-philopatric parental breeding behaviour, the maximum likelihood method implemented in COLONY v2.0.6.5

(Jones and Wang, 2010) was used to infer parent-offspring relationships as well as half and full sibling groupings among all sampled individuals. COLONY input settings were: female and male polygamy with inbreeding; dioecious and diploid; medium length run; full likelihood method; updating of allele frequencies; sibship scaling; no sibship priors. Three replicate runs were conducted with differing seeds and only assignments that were identified with > 90% probability in at least two runs were accepted. Salmonids are not known to display long term monogamous breeding behaviour over extended spatial scales (Taggart et al., 2001) and, thus, full siblings are likely to be the progeny of matings occurring at a single location. Consequently, full siblings should only become separated geographically through post-hatching movement. Half-sibling families can come about in four ways: (1) a single female mates with two or more males in the same place; (2) a single male mates with two or more females in the same place; (3) a single male moves around and mates with two or more females in different places, and (4) a single female moves around and mates with two or more males in different places. Thus, if scenario (3) and (4) occur regularly, the probability that half-siblings hatch in different places should be higher than that for full-siblings. The proportion of groups that contained both inflow and outflow sampled juvenile members was therefore compared between full and half siblings using the prop.test function in R (with ‘sites’ here corresponding to geographic groups, see below). Groups containing Bunaveela-sampled members were excluded from this analysis because our sampling indicates the lake is primarily a feeding habitat for older trout that have already moved to the lake from their natal stream. The null hypothesis of equal proportions corresponds to a situation where there are no pre-hatching differences in spatial distribution of full- versus half-sibling families, or initial differences do exist but are erased by extensive and

random post-hatching movements. A significant difference in proportions (with inflow-outflow mixed site groups more common amongst half siblings) therefore provides indirect evidence for lack of fidelity to a single spawning stream by polygamous parents, coupled with limited movement of fry or parr between inflow and outflow sites.

In order to avoid bias in population structure analyses that can result from the presence of full sibling groups (Rodríguez-Ramilo and Wang, 2012; Rodríguez-Ramilo et al., 2014; Anderson and Dunham, 2008), a single individual was selected from each full sibling group and retained while all other full siblings were excluded from subsequent analyses. PIT-tagged individuals that had been detected on antennae were given preference for retention, followed by individuals with the highest number of scored loci, followed by individuals that had been assigned the highest sample identification number.

Calculating population genetic summary statistics

Prior to conducting population structure analyses, temporally distinct samples were merged based on sampling site where genetic differentiation between sampling years was low. To test for temporal genetic structure within our sampled sites, we calculated within-site between-time pairwise linearised F_{ST} values (Reynolds, Weir and Cockerham, 1983; Slatkin, 1995) and their significance in Arlequin v3.5.2.2 (Excoffier and Lischer, 2010) using 10,000 dememorization steps and a Markov chain length of 100,000. Without any multiple test correction of p-values, no within-site between-time comparisons were significant, and we thus merged samples across years for all sites, resulting in six geographically defined groups (GGs) (Fig. 1 and

Table 2). Each GG was tested for HWE and linkage disequilibrium (LD; a measure of the independence of loci), using the exact G test in GENEPOP (parameters: 10,000 dememorization steps, 100 batches and 1000 iterations per batch). Population summary statistics including observed (H_o) and expected (H_E) heterozygosity, allelic richness (A_R) and inbreeding coefficient (F_{IS}) were calculated for all GGs using the diveRsity package v1.9.90 (Keenan, McGinnity, et al., 2013) in R (Table 2). Private alleles confined to each GG were identified with the poppr package (Kamvar, Tabima and Grünwald, 2014; Kamvar, Brooks and Grünwald, 2015) in R. Effective population size (N_e) was estimated for each GG using the linkage disequilibrium method implemented in NeEstimator V2.1 (Do et al., 2014). This single-sample method has been shown to provide similar or higher precision in estimates of N_e than other available methods when applied to highly polymorphic microsatellite data with limited temporal variation such as those used in this study (Waples and Do, 2010).

Population structure and gene flow

To test for population structure within and among GGs, we used STRUCTURE v.2.3.4 (Pritchard, Stephens and Donnelly, 2000; Falush, Stephens and Pritchard, 2003, 2007; Hubisz et al., 2009) which quantifies individual admixture and does not require the *a priori* grouping of individuals by population. STRUCTURE utilises a Bayesian clustering algorithm to identify the most likely number of distinct genetic clusters (K) within a dataset and determines an individual proportional membership (Q_i) for each sample to the inferred cluster(s) of origin so as to minimise departures from HWE within clusters. A hierarchical approach to STRUCTURE analysis was implemented, whereby major genetic groupings within the dataset were identified and separated from one another prior to investigating subtler genetic structure within

each of these groupings. Because Bunaveela appears to primarily represent a feeding habitat while the inflow and outflow streams are nursery habitats (see results), a model that utilises sampling location as a prior for river samples but not for lake samples and allows for admixture was chosen as the most biologically appropriate for our data. A burn-in period of 100,000 and a Monte Carlo Markov Chain (MCMC) of 1,000,000 repetitions after burn-in was used for each run, and twenty independent iterations with different seed values were conducted for each value of *K* between one and eight. Results from all iterations were analysed with STRUCTURE HARVESTER v0.6.94 (Earl and vonHoldt, 2012) which implements the Evanno method (Evanno, Regnaut and Goudet, 2005) to indicate the most likely value for *K* based on the rate of change in the log probability of data between successive values of *K*. The 'Greedy' algorithm in CLUMPP v1.1.2 (Jakobsson and Rosenberg, 2007) was used to merge the results from each iteration into a combined output file that was used to calculate mean Q_i values as well as to generate bar plots demonstrating individual membership to each STRUCTURE-defined cluster.

In order to identify the likely natal stream (i.e. inflow or upper outflow) of mature lake-feeding trout identified behaviourally as having moved into the inflow only (IO), the outflow only (OO) or both (B), the three behavioural classifications were treated as sampling populations in a STRUCTURE analysis that also included one group comprised of all juveniles sampled in the upper outflow site (GG2) and a second group comprised of all juveniles sampled in the inflow sampling sites (GG4, GG5 and GG6). Location priors were applied to the stream-sampled groups but not to the IO, OO or B groups. This analysis was conducted after purely GG-based analyses had been used to investigate geographic patterns of genetic structure, allowing *K* to be fixed at an appropriate value.

Rates of recent immigration (a proxy for gene flow) between the inflow and the outflow were estimated using BayesAss v3.0.4 (Wilson and Rannala, 2003). BayesAss implements a Bayesian inference framework to estimate the fraction of individuals in a sampled population that are migrants derived from a second (or multiple) sampled population(s) per generation. All samples from the three inflow GGs (GG4, GG5 and GG6) were pooled to form a single 'inflow' group (n = 146), while the upper outflow samples (GG2) formed a second 'upper outflow' group (n = 124). All samples used were from trout that were below the threshold maturity FL at time of sampling, with the majority being young-of-the-year. A burn-in period of 500,000 was used followed by 5,000,000 MCMC iterations with a sampling interval of 1,000 steps. Adjustable acceptance rates fell within the optimal range of 20-60% suggested by Wilson and Rannala without the need to alter mixing parameters. All analyses were conducted 10 times, each with different initial seed values, and the stationary distributions of the associated chains were compared in order to test for convergence between runs.

Broad spatial patterns of genetic differentiation were assessed within the greater Burrishoole catchment in order to test for evidence of isolation by distance (IBD) and explore broad patterns of gene flow between the upper and lower catchment. Pairwise linearized F_{ST} values (Reynolds, Weir and Cockerham, 1983; Slatkin, 1995) and associated p-values were calculated among all GGs in Arlequin and the measuring tool in QGIS (v3.8.0-Zanzibar) was used to measure the minimum traversable waterway distance between all sampling sites. The resulting geographic and genetic distance matrices were assessed for evidence of IBD using a Mantel test (Mantel, 1967) of matrix correspondence as implemented in the 'ape' package v5.2 (Paradis and Schliep, 2018) in R.

Results

Defining maturity status and spawning period

The mean FL of trout that were visually identified as mature during the study period (i.e. ripe, gravid or spent) was 201.2 mm (SD = 36.5 mm, n = 322). We thus set 165 mm as the threshold for designating maturity status (~ mean - 1 SD). At the fish traps, 87.3% of visibly mature trout sampled were above this threshold size. A combination of historical data and recent sampling indicates that outside of the spawning period only 0.46% of trout sampled in the inflow and 0.18% of trout in the upper outflow exceed 165mm, while 26.1% of trout sampled in Bunaveela exceed this length (Supporting Information, Fig. S1).

Growth per GDD of recaptured lake-feeding trout was found to be influenced by both initial FL and T_0. A base temperature of 5°C was selected as the optimum T_0 as model R^2 values peaked at this base temperature ($R^2 = 0.70$). In order to determine individual maturity status, each tagged trout detected on our antennae during a spawning migration period was thus assigned an estimated fork length for the relevant period using the equation

$$FL2 = FL1 + (-0.0303 * \ln(FL1) + 0.1701) * DD5$$

where FL2 is fork length at median date of relevant spawning period, FL1 is fork length at date of initial tagging, and DD5 is the sum of growing degree days above a T_0 of 5°C between both dates. Because growth rate as a function of FL1 followed a von Bertalanffy curve, a logarithmic transformation was applied to FL1 (Hordyk et al., 2014). The equation above accurately predicts the FL of Bunaveela-resident trout that were recaptured more than once during the project and whose intervening

growth between recapture events had been excluded from the model calibration process ($n = 10$, $R^2 = 0.91$, $p < 0.001$, RSE = 6.674).

The vast majority (99.0%) of visibly mature trout captured at the Rough River fish trap during the study period were caught between the dates we designated as the spawning period (1st Nov. to 28th Feb.). Similarly, 96.8% of all detections from mature-sized trout that had been tagged in Bunaveela were recorded on our fluvial antennae between these dates (Supporting Information, Fig. S2).

Behaviour

A total of 456 trout > 70 mm were PIT tagged in Bunaveela during the study period and genetic sex could be confidently determined for 441 of these. Of these, 251 (56.9%) were identified as male and 190 (43.1%) were identified as female. Three hundred and eighty-four trout were tagged prior to the 2017-2018 spawning period and 243 of these were estimated to exceed the size threshold for maturity (165 mm) prior to or during that spawning period. The remaining 72 trout were tagged prior to the 2018-2019 spawning period, by which time 450 of the Bunaveela-tagged trout were estimated to be of mature size. Two hundred and twenty-nine Bunaveela-tagged trout were detected on either the inflow antennae, the outflow antennae, or both. Three of these fish were only detected outside of the designated spawning periods and were excluded from subsequent analyses. A further 18 individuals were classified as being below mature length (i.e. estimated FL2 < 165 mm) during the spawning period in which they were detected and were also excluded from analyses, leaving 208 mature sized individuals that were detected during one or both spawning periods. Together, these fish produced 112,164 individual detections over the two

spawning periods, primarily during the hours of darkness. During the 2017-2018 spawning period, 96.9% and 96.7% of mature trout detections in the inflow and the upper outflow respectively were between sunset and sunrise. During the 2018-2019 spawning period, 93.8% and 89.6% of detections in the inflow and the upper outflow respectively were between sunset and sunrise. One hundred and sixty-nine of the 208 mature length trout that were detected during a spawning period were detected on the outflow antennae (of which 107 were detected exclusively by the upper outflow antennae, i.e. OO fish), 101 were detected on the inflow antennae (39 exclusively on these antenna, i.e. IO fish), and 62 were detected on both inflow and outflow antennae (B fish) (Table 1). Fifty-seven and fifty-eight percent of detected OO and IO fish, respectively, were identified genetically as male, while 64% of B fish were identified as male. The proportion of males within the B group was not found to be significantly different from the proportion of males within the total PIT-tagged group (57%), (Fischer's exact test: $p = 0.18$).

During the study period, three out of 3617 (< 0.1%) trout that were tagged in the lower Burrishoole catchment (i.e. downstream of the lower outflow sampling site) were subsequently detected moving past the upper outflow antennae into Bunaveela. All three individuals had been captured and tagged as they moved downstream through the Rough River trap towards the confluence with the most southerly (downstream) section of the outflow (Fig. 1). None of these fish were detected by the inflow antennae. None of the 577 trout tagged in the inflow, upper outflow and Bunaveela (Supporting Information, Table S2) were detected moving downstream past the lower outflow antenna into the lower catchment nor were any of these fish captured as smolts in the fish traps at the tidal limit.

Table 1. Counts of mature-length trout detected at the upper outflow antennae and the lower inflow antennae during the 2017-18 and the 2018-19 spawning periods.

Antennae	Total	Detected at this stream in both spawning periods	Not detected in other stream in either spawning period	Also detected at other stream either spawning period	Detected at other stream in 17-18 spawning period only	Detected at other stream in 18-19 spawning period only
U_OUTFLOW 2017-18	87	17	46	41	32	5
U_OUTFLOW 2018-19	99	17	69	30	6	22
U_OUTFLOW Both Years	169	17	107	62	34	24
L_INFLOW 2017-18	55	5	17	38	30	2
L_INFLOW 2018-19	51	5	23	28	4	19
L_INFLOW Both Years	101	5	39	62	32	21

Genetics

Parentage and sibship

COLONY identified 52 full-sibling groups with $p \geq 0.9$ within the total successfully genotyped dataset (n = 844) in at least two out of three runs. Full-sibling groups ranged in size from two to 11 individuals. Eighteen groups contained only members sampled in a single stream (inflow or outflow), four groups were dyads containing one inflow and one Bunaveela-sampled member, one group was a dyad containing one upper outflow and one Bunaveela-sampled member, and 29 groups were dyads containing two Bunaveela-sampled members. No full-sibling groups contained both inflow and outflow sampled members. More than 90% of Bunaveela-sampled dyad members were > 85 mm in length (mean FL = 144.3 mm), implying that these Bunaveela-sampled fish were not young-of-the-year and had most likely moved from their natal stream to the lake, unless some lake-spawning had occurred (in contrast, mean FL in stream-sampled groups was 60.1 mm).

Mixed-site groups were relatively frequent amongst half sibling groups compared with full-sibling groups, with 74 out of 163 half-sibling groups (45.4%) composed of

two individuals sampled in separate locations (Table 3). While 61 of these mixed-site half-sibling dyads contained one member sampled in Bunaveela, 11 dyads contained one member sampled in the inflow and a second member sampled in the outflow. In eight of these 11 dyads, both siblings were sampled as young-of-the-year (< 70 mm). When groups containing Bunaveela-sampled members were excluded from analyses (leaving 44 half-sibling groups and 18 full-sibling groups), a significantly higher proportion of half-sibling groups (25%) contained both an inflow and an outflow sampled member compared to full-sibling groups (0%) ($p = 0.049$).

Twenty-four individuals in the total dataset were assigned as parents of other individuals within the dataset (Supporting Information, Table S3). All of these parents were captured within Bunaveela while 12 offspring were sampled in the lake, seven in inflow and five in the upper outflow. Based on the COLONY results, 82 full-sibling samples, representing ~10% of genotyped individuals, were removed from the dataset prior to performing genetic structure analyses in order to prevent full sibling groups from biasing population genetics analyses.

Table 2. Sampling and genetic diversity details of geographic groups (GGs) in the Burrishoole catchment. N is the number of samples in each group, H_E is expected heterozygosity, H_O is observed heterozygosity, N_A is the total number of alleles, A_R is allelic richness, A_P is number of private alleles (i.e. alleles found only in this sampling group), F_{IS} is inbreeding coefficient, N_e is estimated effective population size based on the linkage disequilibrium method.

Sampling Site	GG Code	Sampling Years	N	H_E	H_O	N_A	A_R	A_P	F_{IS}	N_e (95% CI)
Lower Outflow	GG1	2017	27 (27)*	0.72	0.7	120	7.2	21	0.0280 (-0.0587 - 0.1111)	288.90 (98.0-Infinite)
Upper Outflow	GG2	2018	124 (139)*	0.69	0.68	123	6.76	2	0.0141 (-0.0106 - 0.0401)	223.4 (206.8-408.9)
Bunaveela Lough	GG3	2016, 2017, 2018	465 (497)*	0.69	0.69	140	6.98	13	0.0047 (-0.0086 - 0.0183)	756.7 (591.1-1024.8)
Lower Inflow	GG4	2017, 2018	60 (60)*	0.68	0.68	113	6.57	1	0.0032 (-0.028 - 0.0358)	302.8 (159.7-1695.7)
Middle Inflow	GG5	2017, 2018	65 (81)*	0.7	0.72	118	6.74	0	-0.0284 (-0.0613 - 0.0041)	179.3 (120.7-324.5)
Upper Inflow	GG6	2017, 2018	21 (49)*	0.66	0.68	95	6.01	0	-0.0282 (-0.0908- 0.0271)	62.6 (36.7-168.3)

***Note**: Numbers enclosed by brackets in the N column indicate the number of genotyped samples in each GG prior to removal of full siblings samples and samples with < 10 scored loci.

Table 3. Number of between-site and within-site half sibling dyads based on Maximum Likelihood (ML) method in COLONY. Minimum probability required for inclusion of dyad: > 90%.

	Lower Outflow	Upper Outflow	Bunaveela	Lower Inflow	Middle Inflow	Upper Inflow
Lower Outflow	2					
Upper Outflow	2	13				
Bunaveela	7	26	58			
Lower Inflow	0	4	7	0		
Middle Inflow	2	4	15	2	7	
Upper Inflow	0	1	6	1	2	5

Population genetic summary statistics

After pooling temporal samples within sites, and after sequential Bonferroni correction, locus One-102-b showed a significant departure from HWE in the lower outflow group (GG1). No other locus departed significantly from HWE in any other GG, and no locus pairs showed significant LD in any GG. Genetic structure analyses conducted both with and without the One-102-b locus were highly congruent, indicating that this single departure from HWE had no significant impact on

observed patterns of genetic structure between GGs. Consequently, results described hereafter refer to analyses utilising 14 loci, include locus One-102-b.

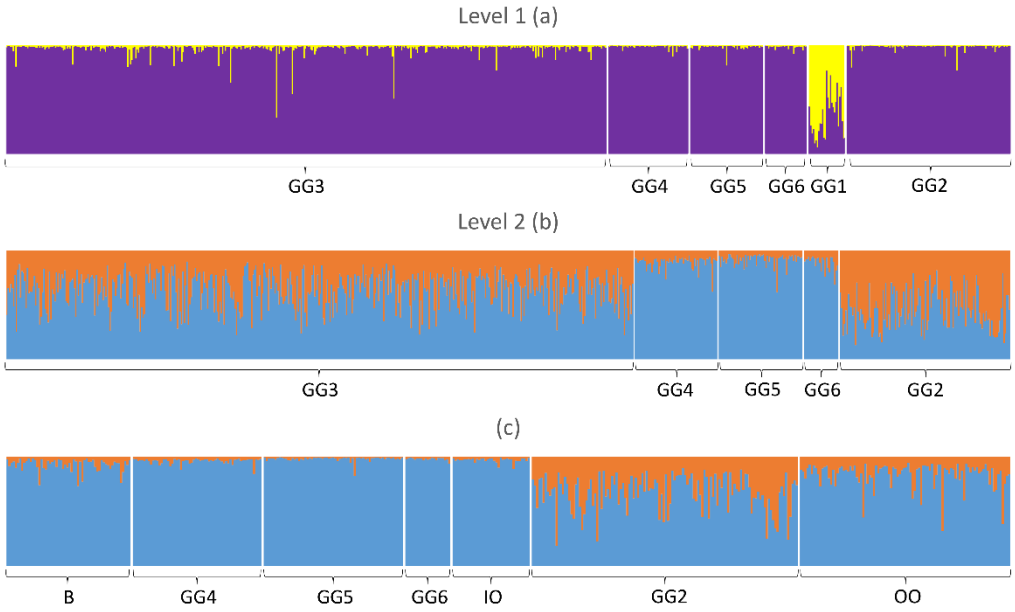


Figure 2. STRUCTURE plot of (a) all 6 GGs (K = 2) (b) 5 upper catchment GGs (GG2-GG6) (K = 2) and (c) pooled inflow GGs (GG4, GG5 and GG6), upper outflow (GG2) and the three behaviourally-defined lake-sampled groups (B = Individuals detected moving into both the inflow and the outflow; IO = Individuals detected moving into the inflow only; OO = Individuals detected moving into the outflow only) (K = 2).

Population structure and gene flow

Level one of hierarchical STRUCTURE analysis identified evidence of two genetic clusters (K = 2) (Supporting Information, Fig. S3 and S4). These two clusters could be broadly described as 'upper catchment' and 'lower outflow'. The upper catchment cluster was predominantly composed of individuals from the five uppermost sampling sites (GG2-GG6), and individuals from these GGs had a mean assignment score (Q_i) to this cluster of 0.97 (SD = 0.06). The lower outflow cluster was

predominantly composed of individuals from the lower outflow (GG1), with lower and more variable individual assignment scores (mean Q_i to the lower catchment cluster was 0.65 ± 0.19) (Fig. 2 a).

In order to investigate lower hierarchical levels of genetic structure within the upper catchment cluster, a STRUCTURE analysis was performed on the five GGs associated with the upper catchment cluster (GG2-GG6). Although the mean ln(*K*) values for this analysis were marginally higher for $K = 1$ than $K = 2$, this difference was minor when compared with all other modelled values of *K*, suggesting that ln(*K*) plateaus at $K = 2$ (Supporting Information, Fig. S5). Furthermore, at $K = 2$, a large proportion of individuals had strong assignment to one cluster or the other, and with spatial non-homogeneity in the distribution of assignment scores (Fig. 2 b), a pattern consistent with the presence of genuine population structure (Pritchard, Wen and Falush, 2007). At $K = 2$, most individuals in the three inflow groups (GG4, GG5 and GG6) assign strongly to a single 'inflow' cluster with low levels of admixture (mean $Q_i = 0.90$, SD = 0.06). In contrast, the Bunaveela and upper outflow (GG3 and GG2) show evidence of significant admixture, with mean inflow cluster Q_i values of 0.64 (SD = 0.16) and 0.45 (SD = 0.17) respectively. These assignment patterns were maintained throughout further STRUCTURE runs in which GG2 (upper outflow) was split into three groups of equal size to the three inflow GGs (Supporting Information, Fig. S7 (a)), but such patterns disappeared when individual samples from the inflow and upper outflow GGs were randomly assigned amongst four predefined groups matched in size to the four donor GGs (Supporting Information, Fig. S7 (b)). These findings indicate that the patterns shown in Fig. 2 represent genuine geographically-based structure rather than artefacts from Bayesian priors.

No evidence of lower hierarchical levels of genetic sub-structuring was detected within the inflow or outflow GGs during subsequent analyses of these groups.

When the OO, IO and B groups of mature PIT-tagged lake-sampled fish were included in a STRUCTURE analysis (fixed at $K = 2$) that also included an upper outflow and a merged inflow group (with the latter two groups composed of fry and parr sampled in the streams), each of the three behaviourally-defined groups exhibited distinct assignment patterns that resemble the characteristic assignment patterns of the inflow and upper outflow groups. In particular, the IO group, the B group and the merged inflow group were characterised by consistently high individual assignment to a single 'inflow' cluster (Fig. 2 c) with mean Q_i values to this cluster of 0.97 (SD = 0.02), 0.90 (SD = 0.06) and 0.97 (SD = 0.02) respectively. In contrast, the OO group and the outflow-sampled juvenile group were both characterised by higher and relatively variable assignment to a second cluster, indicative of greater admixture within these groups (mean Q_i to the second cluster for these groups is 0.17 (SD = 0.11) and 0.33 (SD = 0.16) respectively).

BayesAss results indicate that recent migration rates between the inflow and upper outflow streams have been strongly asymmetrical, and are characterised by a predominantly downstream direction of migration from the inflow to the outflow. Less than 1% (0.95%) of the trout in the inflow are estimated to be migrants derived from the outflow group (per generation), while 32.02% of trout in the upper outflow are estimated to be migrants derived from the inflow group (per generation). The associated 95% credible intervals, a Bayesian analogue to confidence intervals, are 0% to 2.4% and 30% to 34.01% respectively. There was a high degree of convergence between multiple runs (Supporting Information, Table S4), indicating that that the asymmetric pattern detected by BayesAss reflects genuine differences in

migration rates between the inflow and outflow. Genetic diversity generally increased from upstream to downstream, with the minimum A_R recorded in the uppermost group (6.01 in the upper inflow, GG6), and the maximum A_R recorded in the lowest group (7.02 in the lower outflow, GG1).

Table 4. Pairwise genetic distances and geographic distances between all geographic groups (GGs). Genetic distances [$F_{ST}/(1 - F_{ST})$] are located in the bottom left diagonal. Geographic distances (m) are located in the top right diagonal. Genetic distances with significant associated p values (after applying as sequential Bonferroni correction) are indicated by bold text.

	Lower Outflow	Upper Outflow	Bunaveela	Lower Inflow	Middle Inflow	Upper Inflow
Lower Outflow	0	4655	4747	4936	5556	5645
Upper Outflow	**0.02104**	0	92	281	901	990
Bunaveela	**0.01484**	0.00173	0	102	722	811
Lower Inflow	**0.0154**	0.003	0.00042	0	620	709
Middle Inflow	**0.01656**	**0.00443**	0.00179	-0.00166	0	89
Upper Inflow	**0.02835**	**0.01016**	**0.00918**	0.00551	0.00404	0

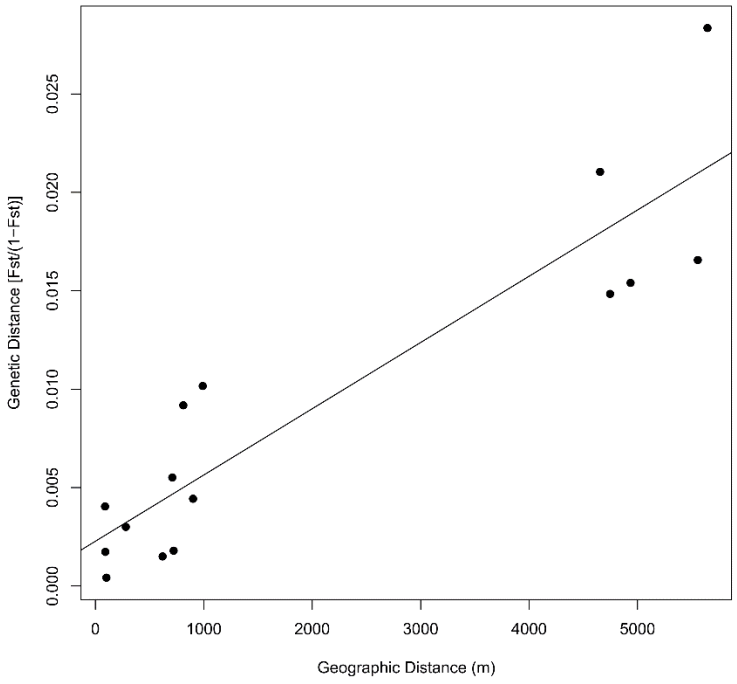


Figure 3. Relationship between genetic distance [F_{ST} / (1 - F_{ST})] and geographic distance (m) for all geographic group (GG) pairings. $R^2 = 0.83$, $p < 0.001$.

Isolation by distance analyses revealed that genetic distance between GG pairs, expressed as Slatkin's pairwise linearized F_{ST} [F_{ST} /(1- F_{ST})], ranged from < 0.001 to 0.028 while geographic distance between sampling sites ranged from 89 m to 5645 m (Table 4). Mantel test results indicate the occurrence of a positive correlation between genetic distance and geographic distance matrices (Z = 525.47, p = 0.013), a pattern of genetic structure consistent with isolation by distance (see Fig. 3). All of the highest pairwise F_{ST} values are associated with GG pairs that include the lower outflow group, GG1 (F_{ST} = 0.015 to 0.029), indicating that the trout sampled at this site belong to the most genetically distinct GG. The lower outflow site is also the most geographically distant site from Bunaveela, located 4747m downstream from the lake. When GG1 was excluded from analysis, the Mantel test revealed evidence of significant IBD within the five upper catchment groups, GG2-GG6 (z-statistic = 25.82, p = 0.033). The three inflow groups (GG4-GG6) share non-significant pairwise F_{ST} values of < 0.006, indicating high rates of gene flow amongst all GGs within the inflowing stream.

Discussion

Previous studies of brown trout have shown that populations spawning in inflowing versus outflowing streams of the same lake are often genetically and phenotypically differentiated, implying limited gene flow among them and potential local adaptation (Massa-Gallucci et al., 2010; Jonsson et al., 1994; Palmé, Laikre and Ryman, 2013; Ferguson and Taggart, 1991; Linløkken, Johansen and Wilson, 2014). In cases where no obvious physical barriers to dispersal exist, some combination of pre-zygotic behavioural isolating mechanisms (that reduce the likelihood of inflow-origin fish straying into outflow streams and successfully mating there, or vice versa) and post-

zygotic ecological barriers (reduced fitness of hybrid offspring) may constrain effective dispersal and thus gene flow. Here we explored these issues at a microgeographic scale, i.e. a fine spatial scale that is within the typical 'dispersal neighbourhood' of the species (Richardson et al. 2014). Our telemetry results showed that the potential for dispersal between inflow and outflow streams is high in the Bunaveela system, given that ~ 30% of lake-tagged trout that were detected by our antennae were detected moving into both streams. Genetic sibship analysis indicated that some fry sampled in nursery habitat in the inflow stream had half-siblings present in the outflow stream (and vice versa), suggesting that one of their parents had reproduced successfully in both streams. This indirect evidence for gene flow was consistent with the rather weak genetic differentiation we documented between the streams. Importantly, however, the genetic data also revealed higher rates of recent migration from the inflow into the outflow than vice versa. Given the short dispersal distances involved and the lack of any obvious physical barriers, our findings point collectively towards interesting asymmetries in pre- or post-zygotic isolating mechanisms, which we discuss further below.

Interpreting the telemetry and population structure results in light of each other

A key goal of this study was to couple PIT-telemetry with microsatellite-based population genetic inference to obtain complementary insights into homing/straying behaviours and the implications for population structuring. *A priori,* we expected to find some genetic differentiation between the inflow and outflow streams, given that (i) brown trout can exhibit genetic structuring at fine spatial scales (Carlsson et al., 1999; Lobón-Cerviá and Sanz, 2017), (ii) previous studies (see above) have found genetic differences between inflow and outflow streams and (iii) isolation by

adaptation mechanisms can be reasonably hypothesised (see below). We indeed documented subtle population structuring within the upper Burrishoole catchment, with two putative clusters that corresponded to some degree, but not perfectly, with inflow versus outflow spawning streams. The weak nature of this structure precluded us from being able to pinpoint cases of 'pure straying' behaviour, which would require assigning lake-tagged individuals with high confidence to a given natal stream (inflow or outflow) and subsequently demonstrating with PIT-telemetry that they were only detected in the opposite stream during the spawning season. However, the existence of 'pure homing' and mixed homing/straying tactics could be tentatively inferred. Lake-tagged fish detected during the spawning period in the inflow stream only (IO group) exhibited consistently high individual assignment (mean Q_i = 0.97, SD = 0.02) to a single putative 'inflow cluster'; thus the IO group, which comprised ~39% of all fish detected on the inflow antennas, likely represented mostly 'inflow-origin homers'.

A second genetic cluster corresponded most closely with the upper outflow (GG2), as indicated by the fact that the mean cluster 2 Q_i for this group was 0.55 (SD = 0.17) in the STRUCTURE analysis that excluded the behavioural groups (Fig. 3 b). The lower and more variable assignment here compared to the very high and consistent assignment of inflow groups (GG4-GG6) to the putative inflow cluster (cluster 1) likely reflects substantial net immigration from inflow to outflow; thus there is weak genetic differentiation between them and high levels of admixture in the outflow. Additional sampling further downstream in the outflow would perhaps have revealed increasing assignment to cluster 2, making the overall distinction with respect to the inflow cluster clearer. When the behavioural groups were included in the analysis, OO fish importantly exhibited higher, although again more variable,

assignments to the putative outflow cluster (mean cluster 2 Q_i = 0.17, SD = 0.11) compared to IO fish (mean cluster 2 Q_i = 0.03, SD = 0.02) or B fish (mean cluster 2 Q_i = 0.10, SD = 0.06). This again indicates admixture in the OO group and suggests that these fish were of mixed ancestry, consistent with gene flow from the inflow to the outflow. Thus OO fish may represent 'outflow-origin homers' (born in outflow, returned to outflow), 'inflow-origin strayers' (born in inflow, moved to outflow), or some mix of both. The genetic assignment patterns point more towards OO fish being predominantly outflow-origin homers, but we have less confidence in this inference relative to our inference regarding the IO fish. Interestingly, the B group were characterised by individual assignment scores to the putative inflow cluster (mean Q_i = 0.90, SD = 0.06) that were lower and more variable relative to IO fish assignments to the same cluster, but higher and less variable relative to OO fish. This suggests that many of the B group fish originated in the inflow stream – having a genetic signature that was more 'inflow in nature' – but may have actually spawned in both streams, again consistent with net gene flow from inflow to outflow. Thus B fish may be both homers and strayers, although clearly the definition of these terms is contingent on the criteria one uses to define 'distinct' genetic populations, which may not map cleanly onto population units defined using demographic criteria (Waples and Gaggiotti, 2006).

The identification of juvenile half-sibling dyads (i.e. sharing a single parent) containing both inflow and outflow sampled fry indicates that some individuals indeed spawn in both streams. An alternative scenario whereby half-siblings were all born in the same stream, but some then moved as fry to the other stream seems highly unlikely, as these fry were sampled early in life on the nursery grounds prior to when extensive dispersion is believed to occur. Additionally, the proportion of

dyads containing both inflow and outflow-sampled members relative to same site dyads was significantly higher amongst half-siblings than amongst full-siblings, indicating that juvenile movement between sites (which is likely to be equally common within half and full sibling groups) does not account for the prevalence of these inflow-outflow half-sibling dyads.

Asymmetric dispersal and the maintenance of genetic structure between inflow and outflow

Bayesian analyses indicated that contemporary migration rates between the two streams is strongly asymmetrical in a predominantly downstream direction, implying that inflow-to-outflow dispersal significantly exceeds outflow-to-inflow dispersal. The programme BayesAss estimated that in recent years, ~ 31% of trout in the upper outflow are migrants derived from the inflow (strayers), which accorded well with our telemetry observation that ~ 37% of ostensible outflow spawners belonged to our B group, i.e. they were detected during the spawning period in both streams. These findings were also consistent with the Bayesian clustering (STRUCTURE) results, whereby juvenile trout sampled in the inflow were characterised by consistently high individual assignment to a single cluster, indicating that effective migrants into this stream are relatively rare. In contrast, fry sampled in the outflow exhibited higher and more variable assignment to a second cluster, indicating that comparatively high rates of immigration result in greater admixture at this location. Taking all genetics and telemetry results together, it appears that trout originating in the inflow are more prone to between-stream dispersal than trout originating in the outflow.

Flow direction effects may combine with behavioural and olfactory mechanisms to bias dispersal in favour of inflow-to-outflow. For example, inflow-born fry may be easily washed downstream into the lake before olfactory imprinting on inflow water, while outflow fry cannot be washed into the lake – they must actively swim against the flow to reach the lake. Additionally, as spawning time approaches, lake-dwelling outflow-origin fish that approach the mouth of the inflow would receive odour cues that 'smell wrong', assuming they first imprinted on outflow water before moving to the lake. In contrast, lake-dwelling inflow-origin fish would presumably detect no odour cues from the outflow stream until they enter it, so such exploratory movements may be more common amongst inflow-origin trout. Moreover, for spawning-age fish of either origin, moving from the lake into the outflow can be completely passive whereas moving into the inflow requires active locomotion.

More generally, asymmetry in gene flow tends to be associated with systems driven by directional physical processes such as flowing water (Sundqvist et al., 2016), wind (Sanmartı, Wanntorp and Winkworth, 2007; Cook and Crisp, 2005), and pelagic currents (Storch and Pringle, 2018; Pringle et al., 2011). In such scenarios, prevailing air or water currents tend to act as pre-zygotic mechanisms that promote dispersal from 'upstream' populations to 'downstream' populations while restricting dispersal in the opposite direction. This asymmetric dispersal coupled with differences in selective pressures (and possible variation in habitat quality) can lead to interesting source-sink population dynamics with complex evolutionary outcomes (Kawecki and Holt, 2002). Additionally, net dispersal from upstream to downstream should lead to higher genetic diversity in downstream populations relative to upstream populations, all else being equal. Indeed, the most downstream group within our set of samples (lower outflow, GG1) exhibited the highest genetic

diversity (Table 2) while the uppermost group (upper inflow, GG6) exhibited the lowest genetic diversity. This broad pattern of decreasing genetic diversity from downstream to upstream suggests that downstream-biased gene flow operates within the Burrishoole catchment at various scales. It is possible that two small waterfalls, the first located upstream of the lower outflow (GG1) and second located just downstream of the upper inflow (GG6), serve to limit upstream gene flow despite being navigable by trout travelling in either direction.

Given putative net gene flow from inflow to outflow, why does the upper outflow not become genetically indistinguishable from the inflow spawning stream? One possibility is that the upper outflow sections receive migrants from genetically distinct subpopulations lower down in the Burrishoole system, but the inflow stream does not, contributing to the maintenance of genetic differences between them. Indeed, a small number of trout that were PIT-tagged in the lower catchment were subsequently detected in the upper outflow, but never in the inflow stream. The genetic contribution of such putative upstream strayers, in conjunction with that provided by downstream strayers from the inflow, may thus account for the pattern of high admixture observed amongst trout sampled in the upper outflow, a pattern that is largely absent from the inflow samples.

An alternative explanation for the maintenance of inflow-outflow genetic differentiation is that reduced fitness of hybrids resulting from matings between inflow- and outflow-origin fish acts as a post-zygotic isolating barrier to effective dispersal. Inflow-born fry must move downstream to reach productive lake-rearing habitat, whereas outflow-born fry must move upstream to reach the lake. A genetic basis for fry movement direction has previously been shown in inflow versus outflow systems (Jonsson et al., 1994), and thus alleles for downstream fry

movement may be selected against in outflow-born hybrids and vice versa in inflow-born hybrids. F1 hybrids may therefore die at higher rates, or grow less well due to not reaching lake habitat, in each stream, effectively reducing rates of gene flow between the streams. Such isolation-by-adaptation processes can also contribute to genetic differentiation at neutral markers, for which divergence is promoted by genetic drift and constrained by gene flow (Nosil, Egan and Funk, 2008; Orsini et al., 2013). The low to moderate N_e values (Table 2) estimated for these populations imply that non-trivial genetic drift may indeed be in operation. The existence of post-zygotic barriers could also foster the evolution of pre-zygotic isolating mechanisms, i.e. reinforcement, where, for example, inflow-origin fish 'prefer' to mate with other inflow-origin fish and vice versa in order to avoid producing less-fit hybrids. It is also worth noting that while the isolation-by-distance pattern we document (Fig. 3) at a broader catchment scale is consistent with simple isolation-by-dispersal-limitation and asymmetric gene flow, it could also be produced by isolation-by-adaptation process if ecological dissimilarity – and therefore the extent of local adaptation – also increases with distance (Orsini et al., 2013).

While our research strongly suggests that mature trout that move from Bunaveela to both the inflow and the outflow often breed successfully in both streams, the nocturnal nature of these activities prevented us from directly observing individuals during spawning. Consequently, we cannot unequivocally confirm that the putative straying behaviour detected during this study resulted in effective dispersal. On the other hand, it is possible for female salmonids to shed PIT tags during spawning (Foldvik and Kvingedal, 2018; Bateman, Gresswell and Berger, 2009; Taylor et al., 2011). Indeed, such tag loss by females may account for the male bias observed

among putative strayers. If so, the actual proportion of strayers amongst the trout tagged during this study may exceed the proportion reported here. Finally, although brown trout primarily spawn in fluvial habitats, they are capable of successfully spawning in lakes if suitable hydrological conditions are present (Arostegui and Quinn, 2019). It is possible that some of the mature sized lake tagged trout that were not detected in either the inflow or outflow were in fact lacustrine spawners. Predation by large brown trout, otters (*Lutra lutra*), eels, cormorants (*Phalacrocorax carbo*) and herons (*Ardea cinerea*) may also account for some of the discrepancy between the number of trout that we tagged and the number we subsequently detected. Due to the difficulty of operating efficient PIT antennae in lakes, and the difficulty of distinguishing lake-feeding from lake-spawning related detections, it was not possible to assess the local prevalence of lake-spawning during this project, nor the influence of such behaviour on local population structure.

Concluding remarks

The geographic scale at which natal philopatry and natal dispersal operate plays an important role in regulating gene flow and determining population structure within the landscape. Our research here indicates that a small expanse of intervening lake habitat can have a significant influence on rates of dispersal and philopatry amongst trout populations that spawn in inflowing and outflowing streams. Furthermore, it appears that in such scenarios inflow-to-outflow dispersal may significantly exceed outflow-to-inflow dispersal. Analogous asymmetric dispersal patterns are found in various species, with important demographic (Storch and Pringle, 2018) and evolutionary (Kawecki and Holt, 2002) consequences. Isolation-by-adaptation type mechanisms may promote the maintenance of genetic differentiation at neutral, in

addition to non-neutral, loci between inflow and outflow populations, whilst asymmetric dispersal will tend to increase genetic diversity of outflow populations. Through these processes, the presence of lake habitat between inflow and outflow streams, despite providing no physical barrier to movement or dispersal, may facilitate the evolution and persistence of local adaptations in salmonid populations at finer geographic scales than has been traditionally suggested in the literature (Adkison, 1995; Fraser et al., 2011). Restocking programmes that fail to adequately consider the geographic scale of local adaptations or the implications of asymmetrical gene flow between captive and wild populations (Baskett and Waples, 2012) may result in sub-optimal performance of stocked fish and potentially threaten the long term performance of extant local populations by diluting locally adapted traits (Mobley et al., 2019; McGinnity et al., 2009, 2007).

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Data availability statement

Sampling data, genetic data, PIT telemetry detection data and growth data are available via the Marine Institute Ireland Data Catalogue, https://doi.org/10.20393/e9395f08-67cb-422a-9ed6-dc16ad5613c8

References

Adkison, M.D., 1995. Population differentiation in Pacific salmon: Local adaptation, genetic drift, or the environment? *Canadian Journal of Fisheries and Aquatic Sciences*, 52, pp.2762–2777.

Anderson, E.C. and Dunham, K.K., 2008. The influence of family groups on inferences made with the program Structure. *Molecular Ecology Resources*, 8(6), pp.1219–1229.

Arostegui, M.C. and Quinn, T.P., 2019. Reliance on lakes by salmon, trout and charr (Oncorhynchus , Salmo and Salvelinus): An evaluation of spawning habitats, rearing strategies and trophic polymorphisms. *Fish and Fisheries*, 20(4), pp.775–794.

Baskett, M.L. and Waples, R.S., 2012. Evaluating alternative strategies for minimizing unintended fitness consequences of cultured individuals on wild populations. *Conservation Biology*, 27(1), pp.83–94.

Bateman, D.S., Gresswell, R.E. and Berger, A.M., 2009. Passive Integrated Transponder Tag Retention Rates in Headwater Populations of Coastal Cutthroat Trout Passive Integrated Transponder Tag Retention Rates in Headwater Populations of Coastal Cutthroat Trout. *North American Journal of Fisheries Management*, 29, pp.653–657.

Boltaña, S., Sanhueza, N., Aguilar, A., Gallardo-escarate, C., Arriagada, G., Valdes, J.A., Soto, D. and Quiñones, R.A., 2017. Influences of thermal environment on fish growth. *Ecology and Evolution*, 7, pp.6814–6825.

Bowler, B., 1975. Factors Influencing Genetic Control in Lakeward Migrations of Cutthroat Trout Fry. *Transactions of the American Fisheries Society*, 3, pp.474–482.

Bradbury, I.R., Hamilton, L.C., Robertson, M.J., Bourgeois, C.E., Mansour, A. and Dempson, J.B., 2013. Landscape structure and climatic variation determine Atlantic salmon genetic connectivity in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(2), pp.246–258.

Brannon, E.L., 1972. *Mechanisms controlling migration of sockeye salmon fry*. New Westminster, Canada.

Carlsson, J., Olsén, K.H., Nilsson, J., Øverli, Ø. and Stabell, O.B., 1999. Microsatellites reveal fine-scale genetic structure in stream-living brown trout. *Journal of Fish Biology*, 55(6), pp.1290–1303.

Chezik, K.A., Lester, N.P. and Venturelli, P.A., 2014. Fish growth and degree-days II: selecting a base temperature for an among-population study. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(9), pp.1303–1311.

Cook, L.G. and Crisp, M.D., 2005. Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *Journal of Biogeography*, 32, pp.741–754.

Dillane, E., McGinnity, P., Coughlan, J.P., Cross, M.C., De Eyto, E., Kenchington, E., Prodöhl, P.A. and Cross, T.F., 2008. Demographics and landscape features determine intrariver population structure in Atlantic salmon (Salmo salar L.): The case of the River Moy in Ireland. *Molecular Ecology*, 17(22), pp.4786–4800.

Dingle, H. and Drake, V.A., 2007. What Is Migration? *BioScience*, 57(2), pp.113–121.

Dionne, M., Caron, F., Dodson, J.J. and Bernatchez, L., 2008. Landscape genetics and hierarchical genetic structure in Atlantic salmon: The interaction of gene flow and local adaptation. *Molecular Ecology*, 17(10), pp.2382–2396.

Dittman, A.H. and Quinn, T.P., 1996. Homing in Pacific salmon: mechanisms and ecological basis. *The Journal of experimental biology*, 199(1), pp.83–91.

Do, C., Waples, R.S., Peel, D., Macbeth, G.M., Tillett, B.J. and Ovenden, J.R., 2014. NeEstimator v2: Re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. *Molecular Ecology Resources*, 14(1), pp.209–214.

Earl, D.A. and vonHoldt, B.M., 2012. STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, 4(2), pp.359–361.

Evanno, G., Regnaut, S. and Goudet, J., 2005. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, 14(8), pp.2611–2620.

Excoffier, L. and Lischer, H.E.L., 2010. Arlequin suite ver 3 . 5 : a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, 10, pp.564–567.

de Eyto, E., Dillane, M., Cooney, J., Hughes, P., Murphy, M., Nixon, P., Sweeney, D., Poole, R. and Rouen, M., 2019. *Water quality and meteorological data from the Lough Feeagh Automatic Water Quality Monitoring Station (AWQMS), 2004-2017 Marine Institute, Ireland*.

de Eyto, E., McGinnity, P., Huisman, J., Coughlan, J., Consuegra, S., Farrell, K.,

O'Toole, C., Tufto, J., Megens, H., Jordan, W., Cross, T. and Stet, R.J.M., 2011. Varying disease-mediated selection at different life-history stages of Atlantic salmon in fresh water. *Evolutionary Applications*, 4, pp.749–762.

Falush, D., Stephens, M. and Pritchard, J.K., 2003. Inference of Population Structure Using Multilocus Genotype Data: Linked Loci and Correlated Allele Frequencies. *Genetics*, 164(4), pp.1567–1587.

Falush, D., Stephens, M. and Pritchard, J.K., 2007. Inference of population structure using multilocus genotype data: Dominant markers and null alleles. *Molecular Ecology Notes*, 7(4), pp.574–578.

Ferguson, A. and Mason, F.M., 1981. Allozyme evidence for reproductively isolated sympatric populations of brown trout Salmo trutta. *Journal of Fish Biology*, 18(6), pp.629–642.

Ferguson, A., Reed, T.E., Cross, T.F., McGinnity, P. and Prodöhl, P.A., 2019. Anadromy, potamodromy and residency in brown trout Salmo trutta : the role of genes and the environment. *Journal of Fish Biology*, 95(3), pp.692–718.

Ferguson, A. and Taggart, J.B., 1991. Genetic differentiation among the sympatric brown trout (Salmo trutta) populations of Lough Melvin, Ireland. *Biological Journal of the Linnean Society*, 43, pp.221–237.

Foldvik, A. and Kvingedal, E., 2018. Long-term PIT tag retention rates in Atlantic salmon (Salmo salar). *Animal Biotelemetry*, 6(3), pp.4–7.

Förschler, M.I., del Val, E. and Bairlein, F., 2010. Extraordinary high natal philopatry in a migratory passerine. *Journal of Ornithology*, 151(3), pp.745–748.

De Fraipont, M., Clobert, J., John-Alder, H. and Meylan, S., 2000. Increased pre-

natal maternal corticosterone promotes philopatry of offspring in common lizards Lacerta vivipara. *Journal of Animal Ecology*, 69, pp.404–413.

Fraser, D.J., Weir, L.K., Bernatchez, L., Hansen, M.M. and Taylor, E.B., 2011. Extent and scale of local adaptation in salmonid fishes: Review and meta-analysis. *Heredity*, 106(3), pp.404–420.

Garant, D., Forde, S.E. and Hendry, A.P., 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology*, 21(3), pp.434–443.

Gomez-Uchida, D., Knight, T.W. and Ruzzante, D.E., 2009. Interaction of landscape and life history attributes on genetic diversity, neutral divergence and gene flow in a pristine community of salmonids. *Molecular Ecology*, 18(23), pp.4854–4869.

Hand, B.K., Muhlfeld, C.C., Wade, A.A., Kovach, R.P., Whited, D.C., Narum, S.R., Matala, A.P., Ackerman, M.W., Garner, B.A., Kimball, J.S., Stanford, J.A. and Luikart, G., 2016. Climate variables explain neutral and adaptive variation within salmonid metapopulations: The importance of replication in landscape genetics. *Molecular Ecology*, 25(3), pp.689–705.

Handeland, S.O., Imsland, A.K. and Stefansson, S.O., 2008. The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. *Aquaculture*, 283, pp.36–42.

Hendry, A.P., Castric, V., Kinnison, M.T. and Quinn, T.P., 2004. The evolution of philopatry and dispersal: Homing versus straying in salmonids. In: A.P. Hendry and S.C. Stearns, eds. *Evolution illuminated: salmon and their relatives*. Oxford and New York: Oxford University Press.

Hilborn, R., Quinn, T.P., Schindler, D.E. and Rogers, D.E., 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences*, 100(11), pp.6564–6568.

Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N.R. and Prince, J., 2014. Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. *ICES Journal of Marine Science*, 72(1), pp.204–216.

Hubisz, M.J., Falush, D., Stephens, M. and Pritchard, J.K., 2009. Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources*, 9(5), pp.1322–1332.

Jacobs, A., Hughes, M.R., Robinson, P.C., Adams, C.E. and Elmer, K.R., 2018. The Genetic Architecture Underlying the Evolution of a Rare Piscivorous Life History Form in Brown Trout after Secondary Contact and Strong Introgression. *Genes*, 280(9), pp.1–23.

Jakobsson, M. and Rosenberg, N.A., 2007. CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, 23(14), pp.1801–1806.

Jones, O.R. and Wang, J., 2010. COLONY: A program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources*, 10(3), pp.551–555.

Jonsson, B. and Jonsson, N., 2001. Polymorphism and speciation in Arctic charr. *Journal of Fish Biology*, 58(3), pp.605–638.

Jonsson, B. and Jonsson, N., 2014. Naturally and hatchery produced European trout

Salmo trutta: Do their marine survival and dispersal differ? *Journal of Coastal Conservation Planning and Management*, 18(2), pp.79–87.

Jonsson, B. and Jonsson, N., 2017. Maternal inheritance influences homing and growth of hybrid offspring between wild and farmed Atlantic salmon. *Aquaculture Environment Interactions*, 9, pp.231–238.

Jonsson, N., Jonsson, B., Skurdal, J. and Hansen, L.P., 1994. Differential response to water current in offspring of inlet and outlet spawning brown trout Salmo trutta. *Journal of Fish Biology*, 45, pp.356–359.

Kamvar, Z.N., Brooks, J.C. and Grünwald, N.J., 2015. Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. *Frontiers in Genetics*, 6, pp.1–10.

Kamvar, Z.N., Tabima, J.F. and Grünwald, N.J., 2014. Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. *PeerJ*, 2, pp.1–14.

Kawecki, T.J. and Ebert, D., 2004. Conceptual issues in local adaptation. *Ecology Letters*, 7, pp.1225–1241.

Kawecki, T.J. and Holt, R.D., 2002. Evolutionary Consequences of Asymmetric Dispersal Rates. *The American Naturalist*, 160(3), pp.333–347.

Kaya, C.M., 1991. Rheotactic differentiation between fluvial and lacustrine populations of Arctic grayling (Thymallus arcticus) implications for the only remaining indigenous population of fluvial 'Montana Grayling'. *Canadian Journal of Fisheries and Aquatic Science*, 48, pp.53–59.

Keefer, M.L. and Caudill, C.C., 2014. Homing and straying by anadromous

salmonids: A review of mechanisms and rates. *Reviews in Fish Biology and Fisheries*, 24(1), pp.333–368.

Keenan, K., Bradley, C.R., Magee, J.J., Hynes, R.A., Kennedy, R.J., Crozier, W.W., Poole, R., Cross, T.F., Mcginnity, P. and Prodöhl, P.A., 2013a. Beaufort trout MicroPlex: A high-throughput multiplex platform comprising 38 informative microsatellite loci for use in resident and anadromous (sea trout) brown trout Salmo trutta genetic studies. *Journal of Fish Biology*, 82(6), pp.1789–1804.

Keenan, K., Mcginnity, P., Cross, T.F., Crozier, W.W. and Prodöhl, P.A., 2013b. diveRsity : An R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods in Ecology and Evolution*, 4(8), pp.782–788.

Kelso, B.W. and Northcote, T.G., 1981. Current response of young rainbow trout from inlet and outlet spawning stocks of a British Columbia lake. *Verhandlungen des Internationalen Verein Limnologie*, 21, pp.1214–1221.

King, R.A., Hillman, R., Elsmere, P., Stockley, B. and Stevens, J.R., 2016. Investigating patterns of straying and mixed stock exploitation of sea trout, Salmo trutta, in rivers sharing an estuary in south-west England. *Fisheries Management and Ecology*, 23(5), pp.376–389.

Lesage, L., Crête, M., Huot, J., Dumont, A. and Ouellet, J., 2000. Seasonal home range size and philopatry in two northern white-tailed deer populations. *Canadian Journal of Zoology*, 78, pp.1930–1940.

Linløkken, A.N., Johansen, W. and Wilson, R.C., 2014. Genetic structure of brown trout, Salmo trutta, populations from differently sized tributaries of Lake Mjøsa in south-east Norway. *Fisheries Management and Ecology*, 21(6), pp.515–525.

Lobón-Cerviá, J. and Sanz, N., 2017. *Brown Trout: Biology, Ecology and Management*. 1st ed. New York: John Wiley & Sons Ltd.

Mantel, N., 1967. The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer Research*, 27(1), pp.2019–220.

Markevich, G., Esin, E. and Anisimova, L., 2018. Basic description and some notes on the evolution of seven sympatric morphs of Dolly Varden Salvelinus malma from the Lake Kronotskoe Basin. *Ecology and Evolution*, 8(5), pp.2554–2567.

Massa-Gallucci, A., Coscia, I., O'Grady, M., Kelly-Quinn, M. and Mariani, S., 2010. Patterns of genetic structuring in a brown trout (Salmo trutta L.) metapopulation. *Conservation Genetics*, 11(5), pp.1689–1699.

McGinnity, P., de Eyto, E., Cross, T.F., Coughlan, J., Whelan, K. and Ferguson, A., 2007. Population specific smolt development, migration and maturity schedules in Atlantic salmon in a natural river environment. *Aquaculture*, 273(2–3), pp.257–268.

McGinnity, P., Jennings, E., DeEyto, E., Allott, N., Samuelsson, P., Rogan, G., Whelan, K. and Cross, T., 2009. Impact of naturally spawning captive-bred Atlantic salmon on wild populations: Depressed recruitment and increased risk of climate-mediated extinction. *Proceedings of the Royal Society B: Biological Sciences*, 276(1673), pp.3601–3610.

McKeown, N.J., Hynes, R.A., Duguid, R.A., Ferguson, A. and Prodöhl, P.A., 2010. Phylogeographic structure of brown trout Salmo trutta in Britain and Ireland: Glacial refugia, postglacial colonization and origins of sympatric populations. *Journal of Fish Biology*, 76(2), pp.319–347.

Mcphee, M. V., Whited, D.C., Kuzishchin, K. V. and Stanford, J.A., 2014. The

effects of riverine physical complexity on anadromy and genetic diversity in steelhead or rainbow trout Oncorhynchus mykiss around the Pacific Rim. *Journal of Fish Biology*, 85(1), pp.132–150.

Mobley, K.B., Granroth-Wilding, H., Ellmen, M., Vähä, J.-P., Aykanat, T., Johnston, S.E., Orell, P., Erkinaro, J. and Primmer, C.R., 2019. Home ground advantage: Local Atlantic salmon have higher reproductive fitness than dispersers in the wild. *Science Advances*, 5(2), pp.1–8.

Moreira, A.L. and Taylor, E.B., 2015. The origin and genetic divergence of "black" kokanee, a novel reproductive ecotype of Oncorhynchus Nerka. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(10), pp.1584–1595.

Neuheimer, A.B. and Taggart, C.T., 2007. The growing degree-day and fish size-at-age : The overlooked metric. *Canadian Journal of Fisheries and Aquatic Science*, 64, pp.375–385.

Neville, H.M., Isaak, D.J., Dunham, J.B., Thurow, R.F. and Rieman, B.E., 2006. Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: Insights from spatial autocorrelation analysis of individual genotypes. *Molecular Ecology*, 15(14), pp.4589–4602.

Nevoux, M., Finstad, B., Davidsen, J.G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O. and Jonsson, B., 2019. Environmental influences on life history strategies in partially anadromous brown trout (Salmo trutta, Salmonidae). *Fish and Fisheries*, 20(6), pp.1051–1082.

Nosil, P., Egan, S.P. and Funk, D.J., 2008. Heterogeneous genomic differentiation between walking-stick ecotypes: 'Isolation by adaptation' and multiple roles for divergent selection. *Evolution*, 62(2), pp.316–336.

Olsen, J.B., Crane, P.A., Flannery, B.G., Dunmall, K., Templin, W.D. and Wenburg, J.K., 2011. Comparative landscape genetic analysis of three Pacific salmon species from subarctic North America. *Conservation Genetics*, 12(1), pp.223–241.

Orsini, L., Vanoverbeke, J., Swillen, I., Mergeay, J. and De Meester, L., 2013. Drivers of population genetic differentiation in the wild: Isolation by dispersal limitation, isolation by adaptation and isolation by colonization. *Molecular Ecology*, 22(24), pp.5983–5999.

Östergren, J. and Nilsson, J., 2012. Importance of life-history and landscape characteristics for genetic structure and genetic diversity of brown trout (Salmo trutta L.). *Ecology of Freshwater Fish*, 21(1), pp.119–133.

Ozerov, M.Y., Veselov, A.E., Lumme, J. and Primmer, C.R., 2012. "Riverscape" genetics: river characteristics influence the genetic structure and diversity of anadromous and freshwater Atlantic salmon (Salmo salar) populations in northwest Russia . *Canadian Journal of Fisheries and Aquatic Sciences*, 69(12), pp.1947–1958.

Palmé, A., Laikre, L. and Ryman, N., 2013. Monitoring reveals two genetically distinct brown trout populations remaining in stable sympatry over 20 years in tiny mountain lakes. *Conservation Genetics*, 14(4), pp.795–808.

Paradis, E. and Schliep, K., 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in {R}. *Bioinformatics*, 35(3), pp.526–528.

Paris, J.R., King, R.A. and Stevens, J.R., 2015. Human mining activity across the ages determines the genetic structure of modern brown trout (Salmo trutta L.) populations. *Evolutionary Applications*, 8(6), pp.573–585.

Perrier, C., Guyomard, R., Bagliniere, J.L. and Evanno, G., 2011. Determinants of hierarchical genetic structure in Atlantic salmon populations: Environmental factors vs. anthropogenic influences. *Molecular Ecology*, 20(20), pp.4231–4245.

Pringle, J.M., Blakeslee, A.M.H., Byers, J.E. and Roman, J., 2011. Asymmetric dispersal allows an upstream region to control population structure throughout a species ' range. *PNAS*, 108(37), pp.15288–15293.

Pritchard, J.K., Stephens, M. and Donnelly, P., 2000. Inference of population structure using multilocus genotype data. *Genetics*, 155(2), pp.945–959.

Pritchard, J.K., Wen, X. and Falush, D., 2007. Documentation for structure software: Version 2.2. *Software: Practice and Experience*, 6(3), pp.321–326.

Prodőhl, P. a, Ferguson, A., Bradley, C.R., Ade, R., Roberts, C., Keay, E.J., Costa, A.R. and Hynes, R., 2019. Impacts of acidification on brown trout populations and the contrubution of stocking to population recovery and genetic diversity. *Journal of Fish Biology*, 95(3), pp.719–742.

Purdue, J.R., Smith, M.H. and Patton, J.C., 2000. Female Philopatry and Extreme Spatial Genetic Heterogeneity in White-Tailed Deer. *Journal of Mammalogy*, 81(1), pp.179–185.

Quinn, T.P., Stewart, I.J. and Boatright, C.P., 2006. Experimental evidence of homing to site of incubation by mature sockeye salmon, Oncorhynchus nerka. *Animal Behaviour*, 72(4), pp.941–949.

Quinn, T.P. and Tallman, R.F., 1987. Seasonal environmental predictability and homing in riverine fishes. *Environmental Biology of Fishes*, 18(2), pp.155–159.

R_Core_Team, 2019. *R: A Language and Environment for Statistical Computing*.

Raleigh, R.F., 1967. Genetic control in the lakeward migrations of sockeye salmon (Oncorhynchus nerka) fry. *Journal of the Fisheries Research Board of Canada*, 24(12), pp.2613–2622.

Raleigh, R.F., 1971. Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. *Ecology*, 52(2), pp.291–297.

Raleigh, R.F. and Chapman, D.W., 1971. Genetic control in lakeward migrations of cutthroat trout fry. *Transactions of the American Fisheries Society*, 1, pp.33–40.

Reynolds, J., Weir, B.S. and Cockerham, C.C., 1983. Estimation of the coancestry coefficient: Basis for a short-term genetic distance. *Genetics*, 105(3), pp.767–779.

Richardson, J.L., Urban, M.C., Bolnick, D.I. and Skelly, D.K., 2014. Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology and Evolution*, 29(3), pp.165–176.

Rodríguez-Ramilo, S.T., Toro, M.A., Wang, J. and Fernández, J., 2014. Improving the inference of population genetic structure in the presence of related individuals. *Genetics research*, 96(July), p.e003.

Rodríguez-Ramilo, S.T. and Wang, J., 2012. The effect of close relatives on unsupervised Bayesian clustering algorithms in population genetic structure analysis. *Molecular Ecology Resources*, 12(5), pp.873–884.

Sanmartı, I., Wanntorp, L. and Winkworth, R.C., 2007. West Wind Drift revisited: testing for directional dispersal in the Southern Hemisphere using event-based tree fitting. *Journal of Biogeography*, 34, pp.398–416.

Schindler, D.E., Armstrong, J.B. and Reed, T.E., 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, 13(5), pp.257–

263.

Slatkin, M., 1995. A Measure of Population Subdivision Based on Microsatellite Allele Frequencies. *Genetics*, 139, pp.457–462.

Stewart, I.J., Quinn, T.P. and Bentzen, P., 2003. Evidence for fine-scale natal homing among island beach spawning sockeye salmon, Oncorhynchus nerka. *Environmental Biology of Fishes*, 67(1), pp.77–85.

Storch, L.S. and Pringle, J.M., 2018. A downstream drift into chaos: Asymmetric dispersal in a classic density dependent population model. *Theoretical Population Biology*, 9, pp.1–9.

Sundqvist, L., Keenan, K., Zackrisson, M., Prodöhl, P. and Kleinhans, D., 2016. Directional genetic differentiation and relative migration. *Ecology and Evolution*, 6(11), pp.3461–3475.

Taggart, J.B., McLaren, I.S., Hay, D.W., Webb, J.H. and Youngson, A.F., 2001. Spawning success in Atlantic salmon (Salmo salar L.): a long-term DNA profiling-based study conducted in a natural stream. *Molecular Ecology*, 10, pp.1047–1060.

Taylor, P., Meyer, K.A., High, B., Gastelecutto, N., Mamer, E.R.J., Steven, F., Meyer, K.A., High, B., Gastelecutto, N., Mamer, E.R.J. and Elle, F.S., 2011. Retention of Passive Integrated Transponder Tags in Stream-Dwelling Rainbow Trout. *North American Journal of Fisheries Management*, 31, pp.236–239.

Taylors, E.B. and Bentzent, P., 1993. Molecular genetic evidence for reproductive isolation between sympatric populations of smelt Osmerus in Lake Utopia, south-western New Brunswick, Canada. *Molecular Ecology*, 2, pp.345–357.

Tonteri, A., Veselov, A.J., Titov, S., Lumme, J. and Primmer, C.R., 2007. The effect

of migratory behaviour on genetic diversity and population divergence: A comparison of anadromous and freshwater Atlantic salmon Salmo salar. *Journal of Fish Biology*, 70((Supplement C)), pp.381–398.

Torterotot, J., Perrier, C., Bergeron, N.E. and Bernatchez, L., 2014. Influence of Forest Road Culverts and Waterfalls on the Fine-Scale Distribution of Brook Trout Genetic Diversity in a Boreal Watershed. *Transactions of the American Fisheries Society*, 143, pp.1577–1591.

Vähä, J.P., Erkinaro, J., Niemelä, E. and Primmer, C.R., 2007. Life-history and habitat features influence the within-river genetic structure of Atlantic salmon. *Molecular Ecology*, 16(13), pp.2638–2654.

Waples, R.S. and Do, C., 2010. Linkage disequilibrium estimates of contemporary Ne using highly variable genetic markers: A largely untapped resource for applied conservation and evolution. *Evolutionary Applications*, 3(3), pp.244–262.

Waples, R.S. and Gaggiotti, O., 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, 15, pp.1419–1439.

Ward, R.D., Woodwark, M. and Skibinski, D.O.F., 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. *Journal of Fish Biology*, 44(2), pp.213–232.

Watkinson, A.R. and Sutherland, W.J., 1995. Sources, sinks and pseudo-sinks. *Journal of Animal Ecology*, 64(1), pp.126–130.

Weatherhead, P.J. and Forbes, M.R.L., 1994. Natal philopatry in passerine birds: Genetic or ecological influences? *Behavioral Ecology*, 5(4), pp.426–433.

Whelan, K.F., Poole, W.R., McGinnity, P., Rogan, G. and Cotter, D., 1998. The Burrishoole System. In: *Studies of Irish Rivers and Lakes, Essays on the occasion of the XXVII Congress of Societas Internationalis Limnologiae (SIL)*. Dublin.pp.191–212.

Wilson, G.A. and Rannala, B., 2003. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics*, 163(3), pp.1177–1191.

Winkler, D.W., Wrege, P.H., Allen, P.E., Kast, T.L., Senesac, P., Wasson, M.F., Llambías, P.E., Ferretti, V. and Sullivan, P.J., 2006. Breeding Dispersal and Philopatry in the Tree Swallow. *The Condor*, 106(4), pp.768–776.

Supporting information

Telemetry and genetics reveal asymmetric dispersal of lake-feeding salmonid between inflow and outflow spawning streams at a microgeographic scale

Table S1. Hydrological properties of Bunaveela Lough, the upper outflow and the inflow streams.

Site	pH	Conductivity µS cm-1	Alkalinity ($CaCO_3$ equivalent mg/l)	Nitrogen (mg/l)	Phosphorous (µg/l)
Bunaveela	7.2	86	33.0	0.657	17.66
Inflow	7.23	116	30.87	0.274	15
Upper Outflow	7.05	96.65	10.14	0.238	7

Table S2. Summary of trout, salmon and char that were caught, tagged or recaptured within the Burrishoole catchment during the duration of the project.

Date	Site	Number of Seine Net Hauls or Electrofishing Passes	Trout Tagged FL >70mm	Trout FL <70mm	Trout Recaptured (previously tagged)	Salmon Tagged FL >70mm	Salmon FL <70mm	Salmon Recaptures (previously tagged)
11/10/2016	Bunaveela	5	44	0	0	10	0	0
12/10/2016	Lodge Stream	3	10	0	0	7	0	0
21/06/2017	Bunaveela	5	147	13	1	29	5	0
23/06/2017	Feeagh	5	71	0	4	80	1	4
28/06/2017	Glenamong River	3	17	0	0	112	0	0
29/06/2017	Lower Outflow	3	28	1	0	139	7	0
16/08/2017	Bunaveela	6	102	16	14	20	2	1
21/08/2017	Feeagh	6	52	0	17	28	3	21
06/09/2017	Lower Inflow	3	20	3	0	8	0	0
06/09/2017	Middle Inflow	3	16	8	0	12	1	0
06/09/2017	Upper Inflow	3	13	10	0	10	6	0
26/10/2017	Bunaveela	6	91	6	19	10	5	1
27/10/2017	Feeagh	6	31	0	12	11	0	9
15/08/2018	Upper Outflow	3	23	129	0	0	0	0
05/09/2018	Lower Inflow	3	28	24	0	0	0	0
05/09/2018	Middle Inflow	3	6	53	0	14	0	0
05/09/2018	Upper Inflow	3	15	12	0	0	0	0
24/10/2018	Bunaveela	4	41	6	10	4	3	0
08/11/2018	Bunaveela	3	31	3	10	2	0	0
27 Dates	Rough River	3	1227	326	315	1111	3539	270
Daily	RR Traps	NA	1759	165	287	546	878	192
Daily	Tidal Limit Traps	NA	450	NA	41	NA	NA	357
	Total	NA	4223	774	730	2153	4450	855

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Table S3. Parentage assignment for offspring from each GG. All parents assigned to offspring within the total dataset came from the Bunaveela GG, including parents of fry sampled in the inflow and outflow streams.

Offspring Site	Bunaveela	Lower Inflow	Middle Inflow	Upper Inflow	Lower Outflow	Upper Outflow	Total
Number assigned to a Bunaveela-sampled parent	12	4	3	0	0	5	24

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Table S4: BayesAss migration estimates between the Inflow and Upper Outflow. 10 runs conducted with different starting seeds in order to assess convergence between runs. m[a][b] describes proportion of immigrants into population [a] derived from population [b] per generation.

	m[UpperOutflow] [Inflow]	m[UpperOutflow] [UpperOutflow]	m[Inflow] [Inflow]	m[Inflow] [UpperOutflow]
Run1	0.3196	0.6804	0.9907	0.0093
Run2	0.3194	0.6806	0.9901	0.0099
Run3	0.3198	0.6802	0.9902	0.0098
Run4	0.3205	0.6795	0.9904	0.0096
Run5	0.3197	0.6803	0.9907	0.0093
Run6	0.3199	0.6801	0.9905	0.0095
Run7	0.3203	0.6797	0.9909	0.0091
Run8	0.3196	0.6804	0.9903	0.0097
Run9	0.3197	0.6803	0.9905	0.0095
Run10	0.32	0.68	0.9907	0.0093
Mean	0.31985	0.68015	0.9905	0.0095
StDev	0.000320156	0.000320156	0.000240832	0.000240832

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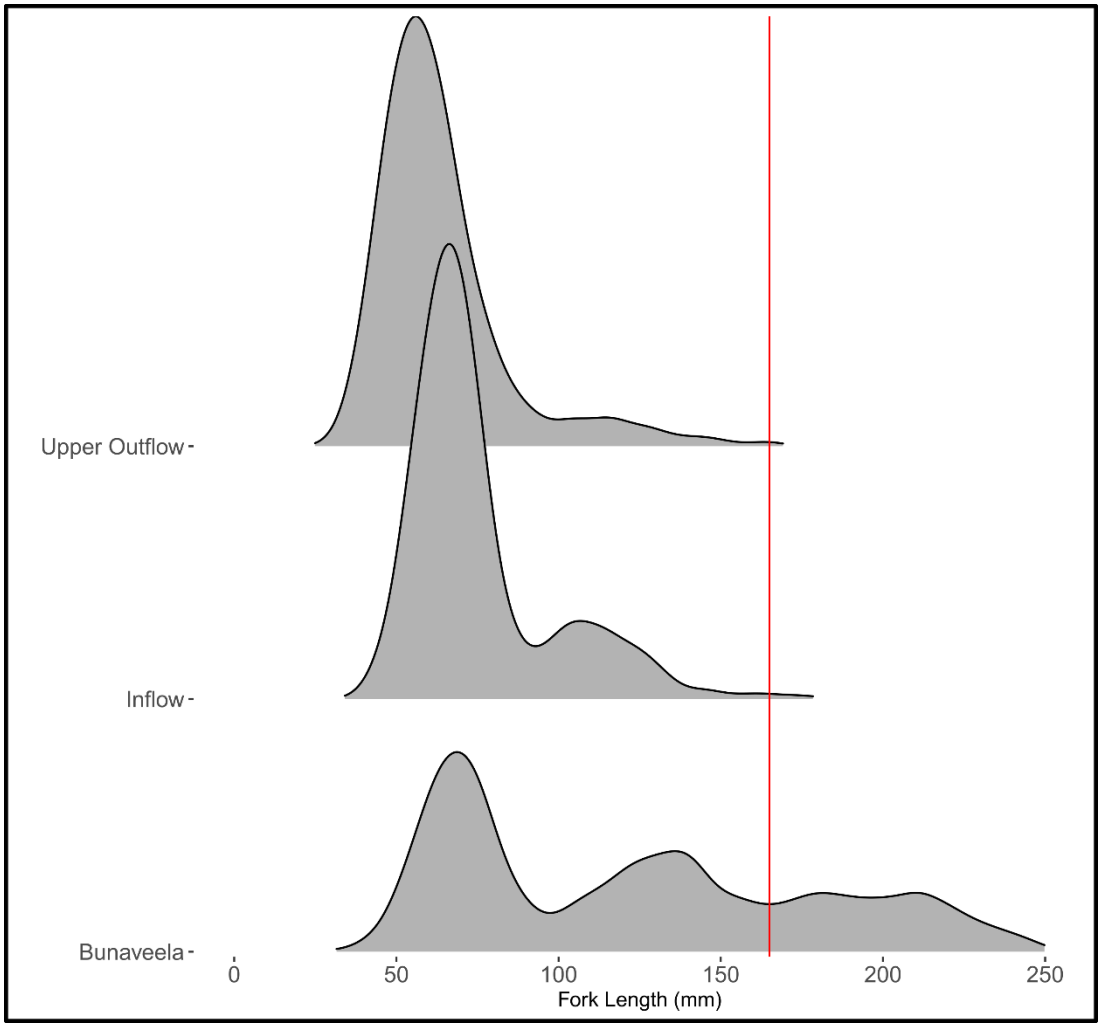


Figure S1. Size distribution (FL) of trout sampled in the inflow (n = 877), the upper outflow (n = 1136) and Bunaveela Lough (n = 3176). The red line at 165 mm represents the threshold length for maturity selected for this study (mean – 1 SD). Sampling period: June-September 1991-2017.

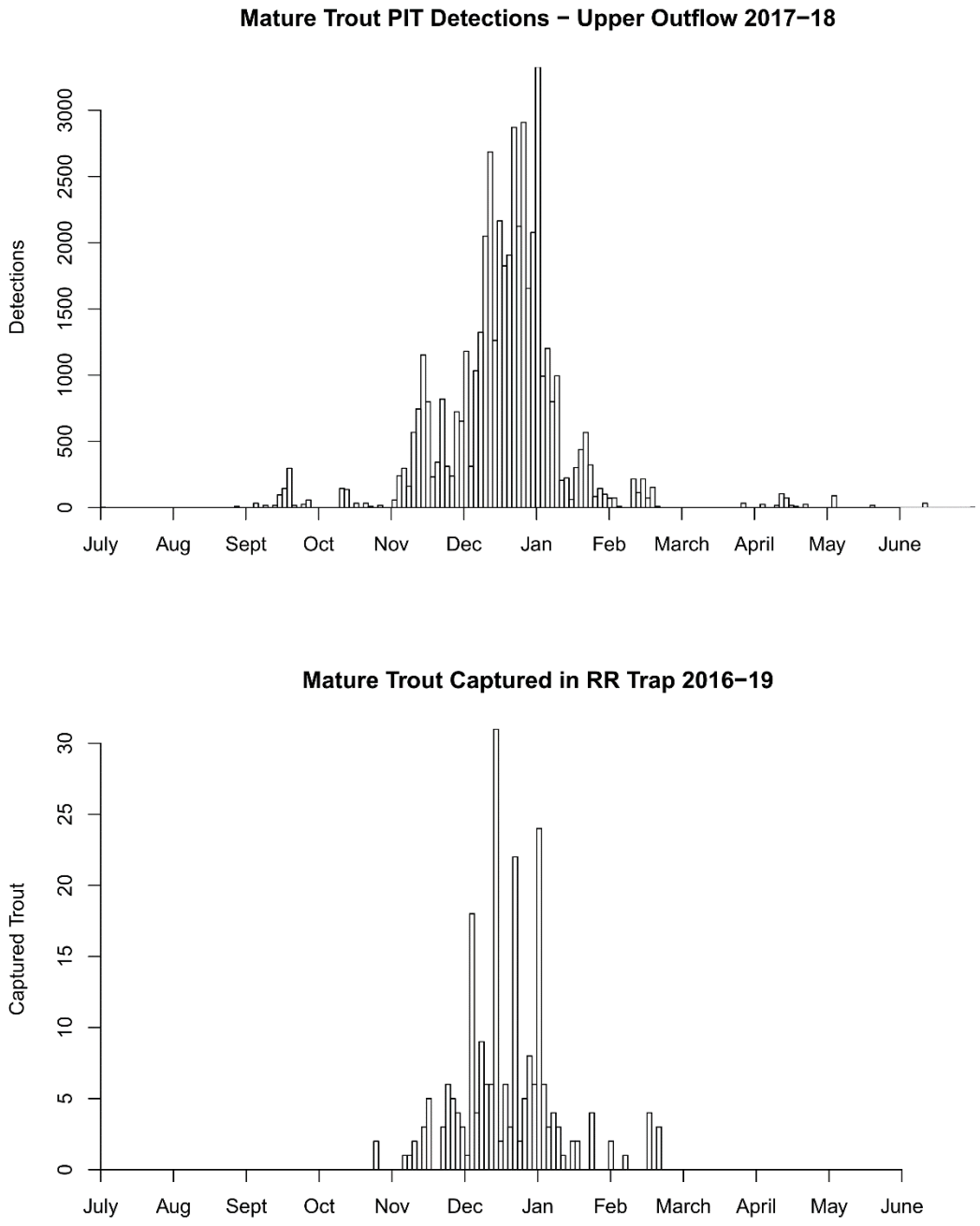
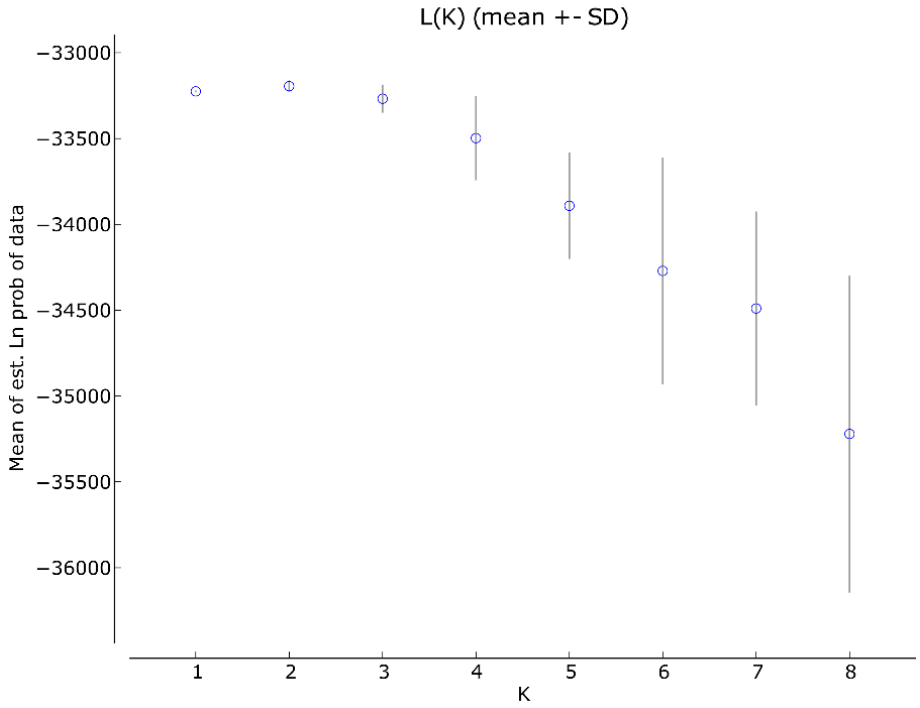


Figure S2. Temporal distribution of PIT detections from mature-sized Bunaveela-tagged trout moving past the upper outflow antennae (July 2017 to June 2018) and phenotypically mature trout (i.e. gravid or ripe) captured at the Rough River fish trap during the study period.



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Figure S3. Mean Ln Probability (STRUCTURE method) of *K* = 1-8. All 6 GGs.

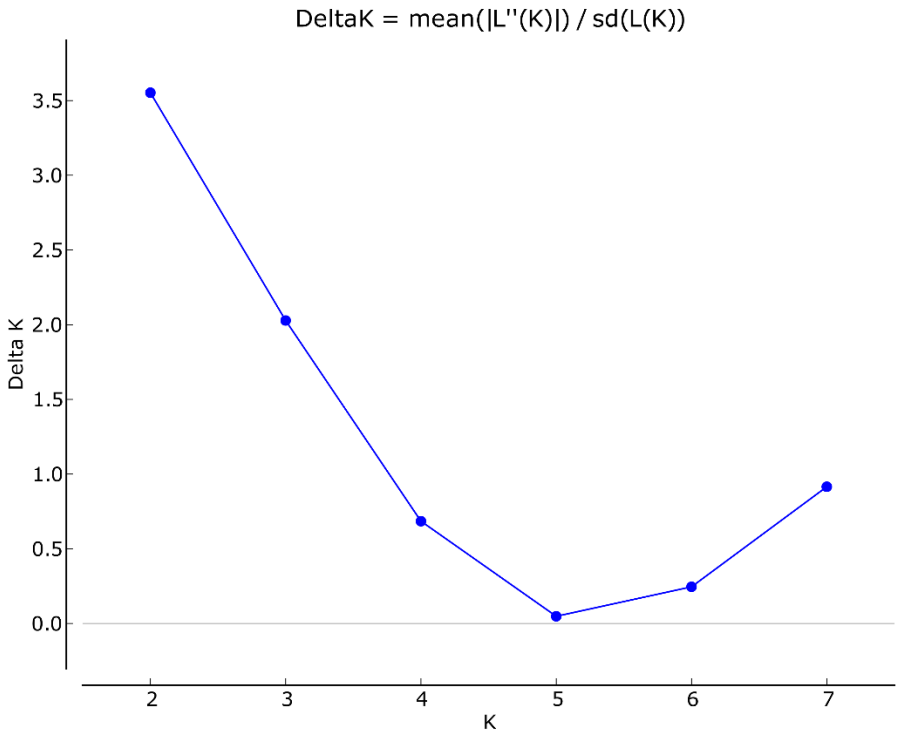


Figure S4. Delta K (Evanno method) of *K* = 2-7. All 6 GGs.

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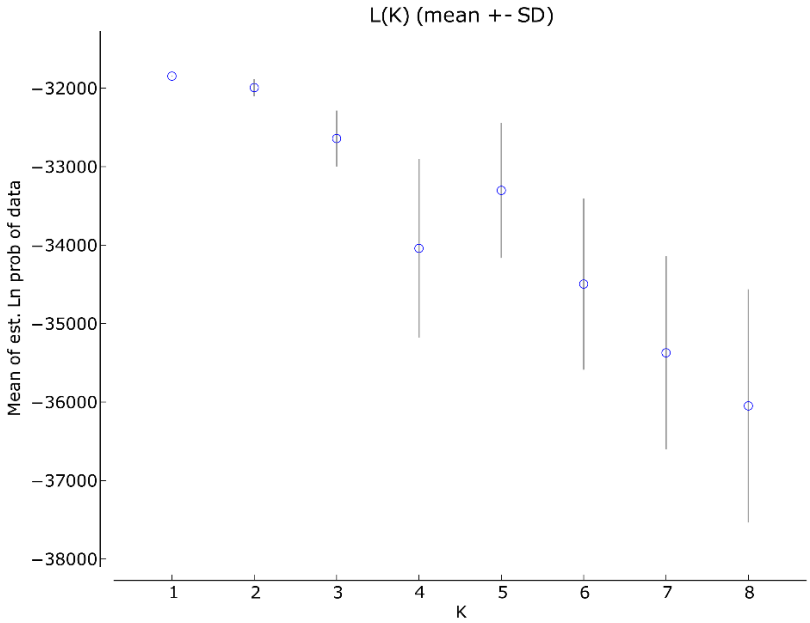
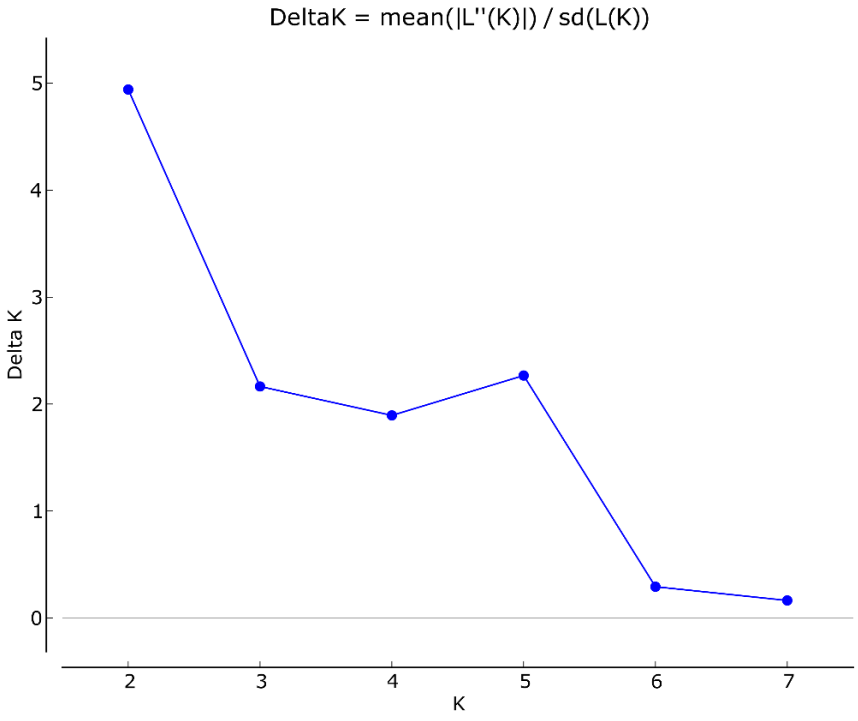


Figure S5. Mean Ln Probability (STRUCTURE method) of *K* = 1-8. GG2-GG6.



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Figure S6. Delta K (Evanno method) of *K* = 2-7. GG2-GG6.

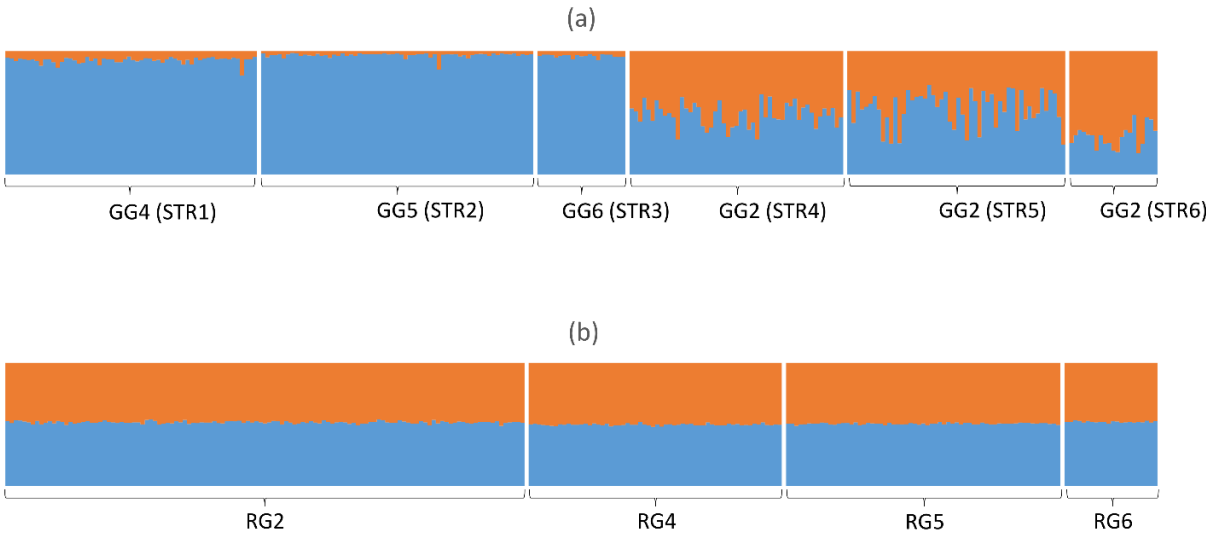


Figure S7. STRUCTURE plots of inflow (GG4-GG6) and upper outflow (GG2) geographic groups (K = 2), in which:

(a) GG2 was divided into three population groups (STR4, STR5 and STR6) equal in size to GG3, GG4 and GG5 prior to analysis.

(b) All samples from the inflow and upper outflow groups (GG2, GG4, GG5 and GG6) were randomly assigned amongst four randomized groups (RGs) equal in size to GG2, GG4, GG5 and GG6 prior to analysis.

General discussion

Environmental heterogeneity is considered to be a primary factor governing the diversity and distribution of organisms globally (Snyder and Chesson, 2004; Palmer, 2003; Stevens and Tello, 2011). Spatial environmental heterogeneity drives adaptation and, ultimately, speciation by providing differing niches, selective pressures and opportunities for reproductive isolation (Stein, Gerstner and Kreft, 2014). Environmental conditions also vary through time over periods ranging from minutes to millennia (Palmer and Poff, 1997). Temporal environmental variation provides distinct challenges to species as resources or tolerable conditions within an area may come and go. As a result, a negative relationship between species richness and temporal heterogeneity is often assumed (Stein, Gerstner and Kreft, 2014).

However, predictable temporal and spatial environmental variations can provide distinct opportunities for species that are capable of moving between habitats. As a result, migratory animals are some of the most successful and abundant organisms on the planet (Swadling, 2006; Wilcove, 2008). The timing, duration, range, direction and frequency of migratory movements displayed by a species or population can be thought of as the evolutionary products of trade-offs amongst innumerable potential life-history strategies (Hansson and Åkesson, 2014). As such, these aspects of migration can yield valuable insights into the proximate and ultimate drivers of animal behaviour throughout our heterogeneous biosphere that provide us with the ability to anticipate, and even ameliorate, the impacts that anthropogenic environmental changes have on migratory species. Against this background, the overarching aim of this thesis was to investigate the interplay between environmental heterogeneity in its broadest sense (i.e. spatial and temporal variation of biotic and

abiotic factors) and locally-adapted migratory behaviours and physiological performance using wild Atlantic salmon and brown trout as case study animals.

Overview of each chapter

The main chapters in this thesis differ substantially from one another in terms of their focus as well as the methodologies they employ. However, each is concerned with a distinct aspect of movement ecology that, together, provide broad insights into the environmental drivers of spatiotemporal variation in the migratory behaviours, migratory performances and genetic structuring found in salmonids.

In Chapter 2 I investigated whether the naturally-occurring infection intensities of the acanthocephalan endoparasite *Pomphorhynchus laevis* had detrimental effects on the physiology of wild Atlantic salmon smolts in either fresh or salt water. Despite causing extensive damage to the intestines of host fish (Wanstall, Thomas and Robotham, 1988; Dezfuli et al., 2008; Wanstall, Robotham and Thomas, 1986; Dezfuli et al., 2002), *P. laevis* had not been associated with mortality or reduced growth in salmonids in previous studies (Wanstall, 1984; Wanstall, Robotham and Thomas, 1986; Hine and Kennedy, 1974). However, all previous studies on the pathological impacts of *P. laevis* infection have been limited to freshwater environments. As has been found with infestations of the freshwater ectoparasite *Gyrodactylus salaris* (Pettersen et al., 2013), I hypothesized that epithelial damage from *P. laevis* infection would lead to reduced hypo-osmoregulatory performance of salmonids in salt water. If severe, such an environmentally-cued (i.e. saltwater specific) pathology could lead to mortality and threaten the persistence of

anadromous salmon populations while increasing selection for freshwater residency in trout. As the Irish strain of *P. laevis* is the only strain of this parasite known to commonly use salmonids as its preferred definitive hosts (O'Mahony, Kennedy and Holland, 2004; Munro, Whitfield and Diffley, 1989; Guillen-Hernandez and Whitfield, 2001), such effects could influence demographic patterns of salmonids in Ireland. However, despite observing high infection intensities of *P. laevis* amongst some the experimental smolts, I found no evidence of an association between infection intensity and mortality, permeability of the gut or variation in the blood parameters I used as indicators of osmoregulatory performance or stress. I did find, however, that the Irish freshwater strain of *P. laevis* can survive for at least 72-hours while their hosts are in salt water, providing a possible explanation for the unusually widespread distribution of the parasite in Ireland. It should be noted, though, that although the salinity of the salt water used in our experimental tanks (~ 26 PPT) was representative of estuarine and coastal waters in Clew Bay, it was lower than in open ocean areas of the Atlantic (~ 35 PPT).

Chapter 3 provides a technical description of a novel double-breakaway pass-through PIT antenna system I developed for use in flood-prone rivers. As described in Chapter 1, PIT telemetry has various advantages over other technologies that are currently used to monitor fish in fluvial environments. However, traditional pass-through PIT antennae are prone to significant and, often, irreparable damage if flotsam becomes entangled in the cables or support ropes. The design that I present in Chapter 3 can withstand high flows and the passage of flotsam without suffering structural damage, saving equipment and labour while minimizing the loss of data. After reliance on traditional pass-through designs led to significant data loss in the early stages of my research, development and adoption of this double-breakaway

design facilitated the collection of data used in chapters 4 and 5 as well as Appendix A.

In Chapter 4 I investigated associations between environmental variables and the seasonal, daily and diel movement patterns of mature brown trout between a feeding lake and two spawning streams (one inflow and one outflow) with the aim of identifying the proximate drivers of temporal spawning movements through transitional areas between habitats. Over two spawning seasons, I used passive integrated transponder (PIT) antennae situated close to the junctions between stream and lake habitat to monitor the movements of mature-sized trout that I had previously PIT tagged in the lake. Movements in both streams were predominantly (89 - 97 %) nocturnal and distinctly seasonal, with a peak in daily detections close to the winter solstice in both years. However, sex-based phenological differences were evident, with male movement activity starting and peaking before that of females (protandry). The probability of detecting either sex increased as stream height rose and as the moon waned, conditions that should increase the ability of migrants to evade visually-oriented predators. These results demonstrate the likely role of temporal environmental heterogeneity in driving the timing of migratory movements over a broad range of scales and provide insights into the evolutionary pressures behind these associations.

The aim of Chapter 5 was to develop our understanding of the finest spatial scales at which genetic structure may arise amongst sympatric migratory salmonids, and to identify the interactions between behaviour and landscape that underlie such structure. To this end, I used a combination of PIT-derived data and genetic analyses to investigate the interplay between gene flow, genetic differentiation and the spawning movements of mature brown trout between the lake and the two streams

mentioned above. As such, it provides insights into the broader implications of some of the findings from Chapter 4. Although nearly 30% of mature individuals entered both streams (and therefore had the opportunity to spawn in both), Bayesian analyses identified the existence of subtle genetic structure amongst juveniles sampled in the two streams and indicated that gene flow was strongly asymmetrical in a predominantly downstream (i.e. inflow to outflow) direction. These findings reveal how, even in the absence of physical barriers to dispersal, spatial environmental heterogeneity can influence migratory behaviour and gene flow patterns at microgeographic scales with potentially important implications for local adaptation and population fitness.

In Appendix A I present some findings from a complementary branch of investigation into freshwater migrations of Atlantic salmon parr and smolts that I pursued during my PhD and that I am preparing for publication in the near future. I describe a small number of these findings in the current discussion (referenced as (Finlay et al., MS in prep.)) in order to highlight the universality or specificity of results described in the preceding chapters.

In Appendix C I present a review of existing literature on the influence of environmental heterogeneity on life history strategies in brown trout with a particular focus on the factors associated with migratory and resident life histories. I was one of 11 authors from an ICES working group on sea trout (WGTRUTTA) involved in writing this paper (providing input to the design and concepts, contributing 15 - 20 % of the text, and proof reading) which forms a relevant synthesis of many of the concepts discussed in the preceding chapters.

The influence of biotic and abiotic components of environmental heterogeneity on life history strategies

Despite its oligotrophic status (de Eyto et al., 2016), the environmental heterogeneity found in the Burrishoole catchment provides its native salmonids with a variety of habitats that offer differing opportunities depending on life stage, season and climatic conditions. The salmon and trout populations that are the focus of Chapters 2, 4 and 5 migrate over a range of temporal and spatial scales in order to take advantage of such heterogeneity. As they grow, trout that hatched in the Fiddaunveela and upper Goulaun streams (Chapter 4 and 5) are likely to find that their access to sufficient food, territory or shelter within their natal habitats becomes increasingly limited. Such limitations account for the near-total absence of mature-sized trout from these streams over nine years of summer electrofishing sampling, while the constant presence of such fish in Bunaveela Lough seine-net surveys (Chapter 4, Fig. S1) indicates that feeding migrations to the lake are a crucial life history strategy for the local trout population(s).

Seine-netting surveys (Chapter 5, Table S2) demonstrate that Bunaveela Lough and Lough Feeagh also provide important growth habitats for salmon parr, particularly those in their second or third year of life. However, despite the evident superiority of Bunaveela Lough to the Fiddaunveela and upper Goulaun streams as a habitat for sustaining growth, records show that only a single trout of over 300 mm (a male of 462 mm) has been captured there during 26 years of seine-net sampling. Thus, even in lacustrine habitats, growth opportunities for salmonids in the Burrishoole catchment appear to be limited and anadromous migrations were once a common life history strategy for the native trout populations. However, severely reduced marine

survival of Burrishoole's anadromous trout since 1989 has been followed by a drastic decline in the output of trout smolts from the catchment despite evidence that freshwater resident trout numbers remain high (Chapter 1, Fig. 1). The development of Atlantic salmon aquaculture in the region in the late 1980s and an associated increase in infestations of *Lepeophtheirus salmonis* is regarded as the primary cause of this sudden reduction in marine survival (Gargan, Tully and Poole, 2003; Tully and Whelan, 1993; Poole et al., 1996, 2007; Whelan, 2010) and demonstrates how changes in the environment (whether biotic or abiotic in nature) may alter the fitness trade-off balance amongst alternate life history strategies and lead to differing behavioural characteristics within and amongst populations.

The freshwater strain of the endoparasite *P. laevis* has a limited and discontinuous distribution (Hohenadler et al., 2018; Roohi, Pazooki and Sattari, 2015; Kennedy, Bates and Brown, 1989) and, furthermore, appears to only use salmonids as its preferred definitive hosts in Ireland (O'Mahony, Kennedy and Holland, 2004; Munro, Whitfield and Diffley, 1989; Guillen-Hernandez and Whitfield, 2001). Accordingly, any pathological effects caused by *P. laevis* to salmonids should primarily impact Irish populations, a pertinent concern given modern declines of anadromous salmonids throughout Ireland (Whelan, 2010). Predominantly infecting non-anadromous fish species (e.g. cyprinids) outside of Ireland (Molloy, Holland and O'Regan, 1995; Ziolkowska et al., 2000; O'Mahony et al., 2004), opportunities for *P. laevis* to move between freshwater catchments are limited. It seems likely that this constraint on colonization routes has contributed to the discontinuous distribution of the freshwater strain of this parasite through much of its range. In contrast, it is possible that the coastal roaming behaviour of Irish anadromous brown

trout amongst neighbouring catchments (Birnie-Gauvin, Thorstad and Aarestrup, 2019) has facilitated the widespread colonization of Ireland by *P. laevis*. Indeed, I found that the *P. laevis* can remain alive in salmonid intestines in salt water environments for at least 72 hours, providing ample time for anadromous trout to move between estuaries and introduce their parasitic passengers to new river systems.

Although I found no evidence to indicate that *P. laevis* affects osmoregulatory performance or stress in Irish salmon smolts in fresh water or within 72 hours of entry into salt water, it is possible that delayed pathologies may occur in salt water when the parasites detach from the intestines, leaving unplugged perforations in their vacated anchoring sites. Such a habitat-specific (i.e. salt water) pathology could negatively impact population performance of obligate anadromous salmonids (i.e. most Atlantic salmon populations) and increase selection for freshwater residency amongst facultative anadromous salmonids such as brown trout. However, given that high infection intensities amongst sampled smolts were not associated with discernible pathologies in fresh or salt water, is also possible that Irish salmonid populations have evolved specific defences that mitigate pathological effects from *P. laevis* infection in both environments. Indeed, Atlantic salmon populations in Sweden and the Baltic region are adapted to withstand high intensity infections of *G. salaris* without suffering significant pathological effects while, in Norway, where the parasite has been recently introduced, similar infection intensities rapidly lead to severe stress, osmoregulatory failure (in salt water) and death amongst native salmon (Johnsen and Jensen, 1991, 1986; Bakke and Harris, 1998).

If Irish salmonids have evolved specific adaptations to *P. laevis* that are absent from salmonid populations in other regions, it is possible that the Irish strain of *P. laevis*

could cause pathologies in foreign populations that were not detected in the Irish experimental smolts. The transportation of live non-native salmonids for the purposes of aquaculture or stocking has been responsible for the introduction of novel diseases and parasites into numerous wild salmon populations, causing severe declines and localised extirpations (Forseth et al., 2017). Furthermore, where native populations are adapted to cope with the parasites or pathogens that are present in their local environment, introgressive hybridization between native salmon and farm escapees may result in reduced population fitness and performance via maladaptation to the pathogenic environment (de Eyto et al., 2011). Such examples serve to highlight the need for grave caution in the regulation of aquaculture or stocking activities, even in cases where fish display no obvious pathologies.

Environmental influences on movement timing, dispersal patterns and genetic structure

Patterns of migration and dispersal across heterogeneous landscapes play an important role in determining potential gene flow patterns and can provide valuable insights into the nature of spatial and temporal selective pressures (O'Toole et al., 2015; Quéméré et al., 2016; Ferguson and Taggart, 1991; Ferguson, 2003). In light of earlier studies that found limited gene flow amongst streams or rivers connected to a shared lake habitat (Massa-Gallucci et al., 2010; Jonsson et al., 1994; Palmé, Laikre and Ryman, 2013; Ferguson and Taggart, 1991; Linløkken, Johansen and Wilson, 2014), my discovery of subtle genetic structure between trout sampled in the inflowing Fiddaunveela and the outflowing upper Goulaun may seem unsurprising. However, given that less than 100 m of lake separates the two streams, the

mechanisms responsible for generating and maintaining genetic differentiation at such a microgeographic scale warrant careful consideration.

Despite evidence of downstream gene flow from the Fiddaunveela (inflow) to the Goulaun (outflow), none of the 584 trout that were tagged in Bunaveela, the Fiddaunveela or the upper Goulaun between 2016 and 2019 were subsequently detected in either the Black River or at the tidal limit fish traps. Three trout that had been tagged in the Rough River (~ 10 km downstream of Bunaveela) were later detected in the upper Goulaun, although none of these were subsequently detected in the Fiddaunveela, indicating that their upstream movements stopped at the lake. These behavioural patterns suggest that upstream dispersal of brown trout from the lower catchment may be significantly reduced by the presence of lacustrine habitat, an inference that is supported by my finding that juveniles sampled in the upper Goulaun were conspicuously admixed while those sampled in the Fiddaunveela, upstream of Bunaveela Lough, exhibited little evidence of admixture.

In contrast to the upstream-moving trout described above, three precocious male salmon that were tagged at the Rough River fish trap were subsequently detected moving up into Bunaveela (an upstream journey of ~ 10 km) and then into the Fiddaunveela over a 72-hour period in December 2018, presumably in search of mating opportunities (Finlay et al., MS in prep.). Such ostensible natal dispersal behaviours may account for the comparative lack of geographically-based genetic structure found amongst Atlantic salmon in the Burrishoole catchment (P. McGinnity, pers. comm.).

A waterfall located in the upper reaches of the Black River historically made the upper Goulaun, Bunaveela and the Fiddaunveela largely inaccessible to salmonids that were downstream of it (Matthews et al., 1997). Despite rudimentary modification works in 1962 and improvements in 1991 that increased the navigability of waterfall in both directions, its presence is likely to have acted as a strong evolutionary force selecting against long-distance downstream migrations from the upper catchment. Thus, as with the apparent effect of salmon farms on rates of anadromy amongst Burrishoole trout (Poole et al., 2007, 1996; Whelan, 2010), this feature of the freshwater environment may account for the ostensible absence (or, at least, rarity) of relatively long-distance or anadromous migratory strategies amongst trout from the upper catchment. Given that the direction of juvenile feeding migrations in brown trout can derive from locally-adapted responses to flow direction (Jonsson et al., 1994), the presence of this waterfall could also have functioned as a post-zygotic ecological barrier to gene flow from the Fiddaunveela to the Goulaun in the sense that Fiddaunveela-Goulaun hybrids that hatched in the Goulaun and migrated downstream (the 'correct' direction for juveniles in the Fiddaunveela) were removed from the gene pool. However, this explanation is not supported by the apparent downstream bias in gene flow from the Fiddaunveela to the Goulaun.

While it is possible that long-distance downstream migration or dispersal from the upper catchment occurs amongst trout that are below tagging size (i.e. < 65-70 mm), and consequently this behaviour was not recorded during my study, it is also possible that locally-adapted plastic responses to environmental heterogeneity could minimise these occurrences while promoting feeding migrations towards Bunaveela Lough from both streams. As discussed in Chapter 4, most of the inflowing

Fiddaunveela stream is significantly shallower than the outflowing Goulaun. Without the moderating influences of the lake, the Fiddaunveela can fade to barely a trickle during droughts and grow to a torrent during heavy rain (R. Finlay, pers. obs.). Given the subtle nature of the genetic structure found between the two streams and the presumed existence of long-term selection against downstream migration past the Goulaun waterfall, it is possible that trout in this area of the catchment are generally adapted to conduct feeding migrations in the direction of positive rheotaxis (i.e. upstream) where possible. In the outflowing Goulaun this movement would lead to a successful outcome (i.e. entry to Bunaveela Lough). Due to the nature of the inflowing Fiddaunveela, upstream moving juvenile migrants will rapidly find their way blocked by impassable barriers such as culverts, rapids and small waterfalls, particularly in periods without rain. Presented with impassable barriers, migrants could exhibit a phenotypically plastic response by reversing their migratory direction and thereby reach the lacustrine feeding habitat of Bunaveela Lough. Additionally, it is possible that the sudden and powerful increases in flow that occur in the Fiddaunveela during heavy rain events cause juvenile trout to be displaced and washed downstream into Bunaveela passively. Indeed, migration and dispersal patterns in numerous species are passively driven by directional environmental forces including wind (Cook and Crisp, 2005; Sanmartı et al., 2007) and ocean currents (Pringle et al., 2011; Storch and Pringle, 2018). Thus, both behavioural and environmental mechanisms could interact to promote lacustrine feeding migrations amongst trout that hatch in the inflowing and outflowing streams and whose populations are connected by some gene flow.

As described in Chapter 4 and 5, the spatiotemporal environmental heterogeneity found between the Fiddaunveela and the Goulaun is associated with somewhat

differing migratory behaviours. In particular, mature trout appear unwilling or unable to move from Bunaveela into the shallow Fiddaunveela during periods of low flows, while, despite a reduction in movement activity, trout continue to move between Bunaveela and the Goulaun during the same periods (Chapter 4, Fig. 2). As a result, trout that originate from the Fiddaunveela may be unable to access their natal stream at times when they are ready to spawn. Given the geographic proximity of the two streams (< 100 m), these impeded Fiddaunveela-origin trout may temporarily abandon natal philopatry and conduct exploratory movements into the outflowing Goulaun where they find and take opportunities to reproduce. These initially exploratory movements could be encouraged by the absence of any 'incorrect' olfactory signals from the outflowing waters. Additionally, if floods in the Fiddaunveela cause fry or parr to be washed into the lake before they imprint on their natal habitat, these individuals should be predisposed to straying (Keefer and Caudill, 2014). Through these processes, environmentally-driven differences in movement timing could contribute to the asymmetrical patterns of gene flow that my analyses revealed. Indeed, ~ 62 % of trout that entered the Fiddaunveela also entered the Goulaun, with genetic analyses indicating that these putative stayers predominantly originated in the Fiddaunveela. Many of the young of the year half sibling groups that were found to be distributed between the two streams are likely to be the progeny of such fish.

The microgeographic genetic structure and downstream-biased gene flow I found between the Fiddaunveela and the Goulaun have broad implications for conservation and fishery management. In particular, my findings suggest that streams that flow into lakes may play an important role in contributing to genetic diversity within outflowing streams. Additionally, the apparently low rates of gene flow into the

Fiddaunveela relative to the Goulaun indicate that populations in inflowing streams can remain genetically distinct from those in nearby outflowing streams. Given that inflowing streams are often smaller and more affected by rapid environmental variations than outflowing streams (Brandt et al., 2017), and given that differing migratory behaviours will provide access to lacustrine habitat, differing selective pressures may lead to the evolution of distinct local adaptations in inflow-spawning populations. Such local adaptations should provide stability to metapopulations encountering environmental changes through their contribution to portfolio effects (Schindler, Armstrong and Reed, 2015). Together these points indicate that the ecological importance of diminutive lake-inflowing streams for salmonids, and perhaps also that of headwaters and tributaries, may be greater than their purely demographic contributions as spawning or nursery habitats would suggest. Consequently, the protection of these habitats and the genetic integrity of their native populations should be a primary concern in fishery management.

As with the spawning migrations of lake-feeding brown trout, I found evidence that environmental heterogeneity in the Burrishoole catchment has strong effects on the timing of downstream movements by migratory salmon smolts (Finlay et al., MS in prep.). Low water levels, or low water temperatures for a given time of year, in Lough Feeagh appear to slow or halt the migratory movements of smolts that had previously moved quite rapidly towards the lake, causing these individuals to spend extended periods in the lacustrine habitat (Appendix A, Fig. 2; 3; 4; 5; 7). Migrants that enter the lake during such conditions can suffer mortality rates in excess of 80 %, while mortality rates during lake passage can drop drastically at times when environmental conditions encourage rapid transit (Appendix A, Fig. 6).

Despite differences in the degree to which spawning movements in the Fiddaunveela and Goulaun were reduced during low rainfall periods, it was apparent from Chapter 4 that photoperiod, stream height and moon phase had similar influences on movement activity in both streams. By primarily moving on nights when the moon provided little illumination and high flows provided cover and depth for passage, these lake-feeding trout reduced their visibility and, presumably, risk of predation while travelling between lacustrine and fluvial habitats. Such behavioural responses to temporal environmental variation are likely to reflect spatiotemporal variation in predation risk posed by the native predator community in the context of the local environment (Bradford and Higgins, 2001; Ovidio et al., 2002; Zavorka et al., 2016; Fraser et al., 1995; Ibbotson et al., 2006; Thorstad et al., 2012). As such, predator avoidance behaviours may be locally adapted and highly specific (Rustadbakken et al., 2004; Hellawell, Leatham and Williams, 1974). Consequently, alterations to the environment (e.g. arterial drainage, flow regulation, water extraction or artificial lighting) or to the predator community (e.g. introduction of non-native predators) may reduce the effectiveness of locally adapted predator avoidance behaviours and lead to decreased population performance (Boulêtreau et al., 2018). Such risks should be considered when assessing the potential impacts of proposed habitat alterations or the movement of species outside their native ranges.

The clear nocturnal bias in spawning-related movements in the Fiddaunveela and the Goulaun was echoed in the nocturnal movements of both adult trout and Atlantic salmon smolts past the Black River antenna (Appendix A, Fig. 8). Interestingly, downstream salmon smolt movements out of Lough Feeagh in 2017, 2018 and 2019 were predominantly diurnal, suggesting that their specific behavioural response to the cyclical signals of sunrise and sunset may vary depending on the habitat they are

currently moving through or from (Finlay et al., MS in prep.). However, previous studies have found that Atlantic salmon smolts can switch from nocturnal migration to diurnal migration as the season progresses, possibly in response to rising water temperatures that increase their ability, as ectotherms, to swim faster and evade predators (Fraser, Metcalfe and Thorpe, 1993; Metcalfe, Fraser and Burns, 1998; Haraldstad et al., 2016). Given that in 2017, 2018 and 2019 smolt movements past the Black River antenna peaked nearly a month before movements out of Lough Feeagh peaked (Appendix A, Fig. 9), the shift from nocturnal to diurnal migration could also be driven by an increase in photoperiod or temperature. The lack of seasonal overlap between detections at the two locations makes it difficult to discriminate between the potential effects of habitat and those of season or temperature, but it seems clear that the observed changes in diel movement patterns were driven by spatial, temporal or spatiotemporal variations in environmental conditions.

The consistency in the distribution of spawning-related movements around the winter solstice that I observed in the Fiddaunveela and the upper Goulaun in both spawning periods despite differences in lake water temperature (Chapter 4, Fig. 2) suggests that the spawning phenology of Bunaveela-feeding trout is entrained by variation in photoperiod. While photoperiod is generally regarded as a primary cue controlling salmonid spawning phenology, individual populations display differing behavioural responses to variation in photoperiod and, thus, differing phenologies (Bromage, Porter and Randall, 2001; García-Vega, Sanz-Ronda and Fuentes-Pérez, 2017; Jonsson and Jonsson, 2011). Locally adapted phenologies should synchronise spawning with a time of year that, on average, provided optimum conditions for embryo development and fry survival upon hatching (Nevoux et al., 2019; Quinn,

Unwin and Kinnison, 2000; Austin, Essington and Quinn, 2019; Quinn and Adams, 1996). However, different selective pressures can drive the phenologies of males and females, commonly resulting in earlier breeding movements of males (Morbey and Ydenberg, 2001; Morbey, 2002, 2000; Esteve, 2005; Jonsson and Jonsson, 2011). Indeed, I documented that Bunaveela-feeding males not only began their spawning movements before females, but that these males were significantly more active (i.e. moved past antennae on more days and more times per day) than females (Chapter 4, Table 1). Given their higher movement frequency and the supposed tendency of male salmonids to roam more widely in search of mates (Aarestrup and Jepsen, 1998; Carss, Kruuk and Conroy, 1990), I was surprised to find that straying rates between the Fiddaunveela and the Goulaun as recorded by our antennae were similar for males and females (Chapter 5). However, the possible environmental drivers of straying behaviour from the Fiddaunveela to the Goulaun that I proposed above are likely to impact males and females equally, and perhaps this accounts for the apparent lack of sex bias in straying rates.

PIT telemetry: Applications and considerations

PIT tags and PIT interrogation devices (i.e. fixed antennae and hand-held scanners) were essential to the research described in Chapter 4 and 5 and revealed the unpublished smolt migration patterns described above (i.e. (Finlay et al., MS in prep.)). Despite its usefulness in fisheries research, though, PIT telemetry has distinct limitations and PIT-based projects can be fraught with frustrations (R. Finlay, pers. obs.). I therefore provide some observations and considerations below that might prove useful when considering or planning a PIT-based project.

Firstly, and most importantly, it is important to decide whether PIT telemetry is capable of providing data that can help answer our research questions. We must therefore be familiar with the inherent limitations of PIT telemetry. Crucially, PIT tags have a limited read range that varies substantially depending on tag type (HDX or FDX), tag size (i.e. 8mm, 12mm, 23mm and 32mm), tag orientation, tag movement speed, reader type (handheld vs in-stream antennae), antenna size, antenna shape, antenna pulse rate, antenna tuning, antenna inductance, antenna voltage, local geology, water conductivity, environmental or electrical noise and, it often seems, a variety of unquantifiable and indefinable factors. However, as an example, a decent homemade HDX antenna measuring 60 cm X 300 cm in a low noise environment and incorporating modern interrogation components from Oregon RFID should be capable of detecting 12 mm tags (as commonly used in juvenile salmonids) from at least 35 cm away (i.e. upstream and downstream), providing a 70 cm reading window and perhaps 8 cm of additional interrogation area around the outside of the antenna loop. The pulse rate of the antenna and the expected speed of tag movement can be used to calculate whether tags in fish are likely to be detected within the read window. Intended study organisms (or inorganic objects) must be suitable for tagging, and the correct sized tag must be implanted in the correct location. As an example, salmonids can expel intraperitoneal PIT tags during spawning (Prentice, Flagg and McCutcheon, 1990; Bateman, Gresswell and Berger, 2009), so intramuscular tag placement (which is unsuitable for small fish) may provide longer tag retention in adult fish.

Secondly, we must choose whether to use full-duplex (FDX) or half-duplex (HDX) tags, and this will dictate what interrogation systems we can use. A full-duplex antenna generates a continuous magnetic field, providing power to nearby FDX tags

which respond immediately by transmitting their unique ID number at up to 30 times per second. A half-duplex antenna generates short magnetic pulses (usually ≤ 15 per second) that charge a capacitor inside any nearby HDX tag. When the charge field turns off, the tag uses its stored power to send its ID number back to the antenna without interference from the antenna's magnetic field. HDX antennae are much simpler and cheaper to construct, are generally more robust, and can be made significantly larger than equivalent FDX systems. HDX systems are the obvious choice for many projects with limited budgets, where flexibility in antenna dimensions is beneficial or where wide or volatile rivers must be spanned. FDX systems are usually custom built by manufacturers and are significantly more complicated and expensive to construct, although they do provide faster read speeds. Consequently, FDX systems are particularly useful in manmade fish passes where many tagged fish may rapidly move past an antenna over a brief period.

Thirdly, if planning to install an in-stream antenna, serious thought should be given to site selection. I provide a number of considerations below regarding site selection in order of, in my opinion, their importance.

1. Research question: Will detections at the location help answer the research question? As an example, antennae arrangements suitable for studying behaviour or phenology may be unsuitable for studying aspects of survival (and vice versa). A single antenna, for instance, does not give any information on the direction of travel.

2. Accessibility: Is there suitable access to the site? Most remote PIT systems are powered by multiple heavy (i.e. > 30 kg) batteries that must be swapped out periodically. Vehicle access to, or close to, the installation site is invaluable in such situations! Other options are available to power antennas in remote sites (i.e. solar panels, gas turbines, diesel generators etc.) but these are often costly and complicated to install and may reduce detection efficiency by introducing noise into the system.
3. Riverine conditions: Does the profile and composition of the riverbed and banks provide suitable conditions to secure an effective antenna that will withstand expected flow conditions and flotsam? Ideal locations for pass-through antenna have a flat streambed, vertical banks and a substrate that can securely hold antenna supports. Additionally, power sources and unsealed electronics must be located above the water level during the largest anticipated floods, so access to nearby high ground may be required.
4. Noise: Is the site affected by high noise? Noise reduces the performance (read range) of PIT antennae and can be generated by nearby electrical equipment (radiated noise), vibrations in the environment or small voltage variations in the power supply (conducted noise). High noise sites should be avoided where possible.

Finally, when considering PIT antenna installations and designs, we must choose between pass-by (or 'flat-bed') and pass-through (or 'swim-through') orientations. Flat-bed antennae lie flat on the streambed, providing less exposure to the current and suspended flotsam. As such, a flat-bed antenna will generally encounter less strain than a similar sized pass-through antenna in the same location. However, the

horizontal orientation of flat-bed antennae severely reduces their vertical read range. If study animals are likely to travel more than ~ 20 cm above stream bed, pass-through antennae are likely to provide much higher detection efficiency than flat-bed designs although frequent damage from flotsam can make traditional pass-through antennae unfeasible in some locations. The double-breakaway antenna system described in Chapter 3 can facilitate the use of pass-through designs in these locations.

Conclusions, limitations and future research

The results presented in this thesis reveal how spatiotemporal variation in abiotic and biotic components of the natural environment can influence movement patterns, gene flow and physiological performance of migratory populations. However, my findings and the implicit limitations of my research have opened up various new avenues for future research.

In Chapter 2 I showed that the Irish freshwater strain of *P. laevis* can survive for a minimum of 72 hours while its host is in salt water, although I found no evidence of parasite-induced pathologies. However, the salinity and timeframe in my experimental tanks was only 26 PPT (representative of local coastal waters experienced by the smolts during the first couple of days outside freshwater) and 72 hours, reducing hypo-osmoregulatory demands on the experimental smolts and potentially providing a more tolerable internal environment for *P. laevis* compared with full salinity sea water. Similar experiments conducted over a longer time-span in water with a salinity of ~ 35 PPT could help determine the maximum lifespan of

P. laevis in Atlantic salmon in an open ocean environment (with implications for potential colonization patterns) and, crucially, reveal whether delayed marine pathologies occur when these parasites vacate the intestines. Additionally, given the consistently low marine survival of trout from the Burrishoole catchment in recent decades, it would be interesting to investigate whether *P. laevis* causes such habitat-specific pathologies in brown trout.

In Chapter 4 I revealed strong associations between the timing of spawning-related movements and photoperiod, moon phase and water height, concluding that the fine-scale timing of movements through transitional habitat was likely to represent an evolved response to temporal variation in visibility and predation risk. However, moon phase is a somewhat imprecise indicator of illumination at night, with the distance of the moon from the Earth and the timing of moonrise and moonset interacting with cloud cover to determine brightness at any particular moment. Additionally, my use of water height data from a nearby stream as a proxy for heights in the Fiddaunveela and the Goulaun may have reduced the strength of associations between stream height and activity in my models. However, this should not undermine the methodology or the findings in this analysis. In the future, it would be interesting to use direct measures of brightness and water height or flow rate in such streams throughout the day to determine the precise degree of synchronisation between these environmental factors and fine-scale temporal movement patterns. Such a study could also incorporate a measure of predation, spawning success or migrant survival, thereby providing direct evidence of the evolutionary advantages of these environment-cued movement behaviours.

In Chapter 5 I revealed that subtle genetic structure and asymmetrical downstream-biased gene flow patterns can occur between brown trout in streams that are

separated by less than 100 m of lake habitat. In addition, I recorded ostensible straying patterns that provide a plausible behavioural explanation for these genetic patterns. However, without the opportunity to sample eggs in redds, I used sibship analyses of mobile juveniles sampled in the summer to test for more direct evidence of multi-river spawning (i.e. straying). While it is likely that these juveniles had not moved from their natal stream at the time of sampling (see Chapter 5), sampling of eggs in spawning beds would have provided greater certainty. Finally, while it is known that various trout populations spawn in lake habitats (Arostegui and Quinn, 2019), this potentially important component of trout biology is relatively unstudied. Given my findings on genetic structure and spawning behaviour between the inflowing Fiddaunveela and the outflowing Goulaun, it would be very interesting to determine the role, if any, that lake spawning has in maintaining local demographic and genetic patterns.

References

Aarestrup, K. and Jepsen, N., 1998. Spawning migration of sea trout (Salmo trutta (L)) in a Danish river. *Hydrobiologia*, 371, pp.275–281.

Arostegui, M.C. and Quinn, T.P., 2019. Reliance on lakes by salmon, trout and charr (Oncorhynchus , Salmo and Salvelinus): An evaluation of spawning habitats, rearing strategies and trophic polymorphisms. *Fish and Fisheries*, 20(4), pp.775–794.

Austin, C.S., Essington, T.E. and Quinn, T.P., 2019. Spawning and emergence phenology of bull trout Salvelinus confluentus under differing thermal regimes. *Journal of Fish Biology*, 94(1), pp.191–195.

Bakke, T.A. and Harris, P.D., 1998. Diseases and parasites in wild Atlantic salmon (Salmo salar) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(1), pp.247–266.

Bateman, D.S., Gresswell, R.E. and Berger, A.M., 2009. Passive Integrated Transponder Tag Retention Rates in Headwater Populations of Coastal Cutthroat Trout Passive Integrated Transponder Tag Retention Rates in Headwater Populations of Coastal Cutthroat Trout. *North American Journal of Fisheries Management*, 29, pp.653–657.

Birnie-Gauvin, K., Thorstad, E.B. and Aarestrup, K., 2019. Overlooked aspects of the Salmo salar and Salmo trutta lifecycles. *Reviews in Fish Biology and Fisheries*, 29, pp.749–766.

Boulêtreau, S., Gaillagot, A., Carry, L., Tétard, S., De Oliveira, E. and Santoul, F., 2018. Adult Atlantic salmon have a new freshwater predator. *PLoS ONE*, 13(4),

pp.1–12.

Bradford, M.J. and Higgins, P.S., 2001. Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Oncorhynchus mykiss). *Canadian Journal of Fisheries and Aquatic Science*, 58, pp.365–374.

Brandt, M.J., Johnson, K.M., Elphinston, A.J. and Ratnayaka, D.D., 2017. Dams and Reservoirs. In: *Twort's Water Supply*, 7th Editio. Butterworth-Heinemann.pp.159–204.

Bromage, N., Porter, M. and Randall, C., 2001. The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. *Aquaculture*, 197(1–4), pp.63–98.

Carss, D.N., Kruuk, H. and Conroy, J.W.H., 1990. Predation on adult Atlantic salmon, Salmo salar L., by otters, Lutra lutra (L.), within the River Dee system, Aberdeenshire, Scotland. *Journal of Fish Biology*, 37, pp.935–944.

Dezfuli, B.S., Lui, A., Boldrini, P., Pironi, F. and Giari, L., 2008. The inflammatory response of fish to helminth parasites. *Parasite*, 15(3), pp.426–433.

Dezfuli, B.S., Pironi, F., Giari, L., Domeneghini, C. and Bosi, G., 2002. Effect of Pomphorhynchus laevis (Acanthocephala) on putative neuromodulators in the intestine of naturally infected Salmo trutta. *Diseases of Aquatic Organisms*, 51, pp.27–35.

Esteve, M., 2005. Observations of Spawning Behaviour in Salmoninae: Salmo , Oncorhynchus and Salvelinus. *Reviews in Fish Biology and Fisheries (2005)*, 15, pp.1–21.

de Eyto, E., Dalton, C., Dillane, M., Jennings, E., McGinnity, P., O'Dwyer, B., Poole, R., Rogan, G. and Taylor, D., 2016. The response of North Atlantic diadromous fish to multiple stressors, including land use change: a multidecadal study. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(12), pp.1759–1769.

de Eyto, E., McGinnity, P., Huisman, J., Coughlan, J., Consuegra, S., Farrell, K., O'Toole, C., Tufto, J., Megens, H., Jordan, W., Cross, T. and Stet, R.J.M., 2011. Varying disease-mediated selection at different life-history stages of Atlantic salmon in fresh water. *Evolutionary Applications*, 4, pp.749–762.

Ferguson, A., 2003. Brown trout genetic diversity : origins, importance and the impacts of supplemental stocking. In: *Proceedings of the Institute of Fisheries Management 34th Annual Study Course*. pp.26–43.

Ferguson, A. and Taggart, J.B., 1991. Genetic differentiation among the sympatric brown trout (Salmo trutta) populations of Lough Melvin, Ireland. *Biological Journal of the Linnean Society*, 43, pp.221–237.

Forseth, T., Barlaup, B.T., Finstad, B., Fiske, P., Gjøsæter, H., Hindar, A., Mo, T.A., Rikardsen, A.H. and Thorstad, E.B., 2017. The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science*, 74(6), pp.1496–1513.

Fraser, N.C., Metcalfe, N.B. and Thorpe, J.E., 1993. Temperature-Dependent Switch between Diurnal and Nocturnal Foraging in salmon. *Proceedings of the Royal Society B: Biological Sciences*, 252, pp.135–139.

Fraser, N.H.C., Heggenes, J., Metcalfe, N. and Thorpe, J.E., 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. *Canadian Journal of Zoology*, 73, pp.446–451.

García-Vega, A., Sanz-Ronda, F.J. and Fuentes-Pérez, F.J., 2017. Seasonal and daily upstream movements of brown trout Salmo trutta in an Iberian regulated river. *Knowledge and Management of Aquatic Ecosystems*, 418(9), pp.1–9.

Gargan, P.G., Tully, O. and Poole, W.., 2003. Relationship between sea lice infestation, sea lice production and se trout survival in Ireland, 1992-2001. In: D. Mills, ed. *Salmon on the Edge*. Oxford, UK: Blackwell Publishing Ltd.pp.119–135.

Guillen-Hernandez, S. and Whitfield, P.J., 2001. A comparison of freshwater and marine/ estuarine strains of Pomphorhynchus laevis occurring sympatrically in flounder, Platichthys flesus, in the tidal Thames. *Journal of Helminthology*, 75, pp.237–243.

Hansson, L.-A. and Åkesson, S., 2014. *Animal Movement Accross Scales*. Oxford: Oxford University Press.

Haraldstad, T., Kroglund, F., Kristensen, T., Jonsson, B. and Haugen, T.O., 2016. Diel migration pattern of Atlantic salmon (Salmo salar) and sea trout (Salmo trutta) smolts: an assessment of environmental cues. *Ecology of Freshwater Fish*, 26(4), pp.541–551.

Hellawell, J.M., Leatham, H. and Williams, G.I., 1974. The upstream migratory behaviour of salmonids in the River Frome, Dorset. *Journal of Fish Biology*, 6, pp.729–744.

Hine, P.M. and Kennedy, C.R., 1974. Observations on the distribution, specificity and pathogenicity of the acanthocephalan Pomphorhynchus laevis (Muller). *Journal of Fish Biology*, 6, pp.521–535.

Hohenadler, M.A.A., Nachev, M., Thielen, F., Taraschewski, H., Grabner, D. and

Sures, B., 2018. Pomphorhynchus laevis: An invasive species in the river Rhine? *Biological Invasions*, 20, pp.207–217.

Ibbotson, A.T., Beaumont, W.R.C., Pinder, A., Welton, S. and Ladle, M., 2006. Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. *Ecology of Freshwater Fish*, 15, pp.544–551.

Johnsen, B.O. and Jensen, A.J., 1986. Infestations of Atlantic salmon, Salmo salar, by Gyrodactylus salaris in Norwegian rivers. *Journal of Fish Biology*, 29(2), pp.233–241.

Johnsen, B.O. and Jensen, A.J., 1991. The Gyrodactylus Story in Norway. *Aquaculture*, 98(1–3), pp.289–302.

Jonsson, B. and Jonsson, N., 2011. *Ecology of Atlantic salmon and brown trout: Habitat as a template for life histories*. Dordrecht: Springer Netherlands.

Jonsson, N., Jonsson, B., Skurdal, J. and Hansen, L.P., 1994. Differential response to water current in offspring of inlet and outlet spawning brown trout Salmo trutta. *Journal of Fish Biology*, 45, pp.356–359.

Keefer, M.L. and Caudill, C.C., 2014. Homing and straying by anadromous salmonids: A review of mechanisms and rates. *Reviews in Fish Biology and Fisheries*, 24(1), pp.333–368.

Kennedy, C.R., Bates, R.M. and Brown, A.F., 1989. Discontinuous distributions of the fish acanthocephalans Pomphorhynchus laevis and Acanthocephalus anguillae in Britain and Ireland : an hypothesis. *Journal of Fish Biology*, 34, pp.607–619.

Linløkken, A.N., Johansen, W. and Wilson, R.C., 2014. Genetic structure of brown trout, Salmo trutta, populations from differently sized tributaries of Lake Mjøsa in

south-east Norway. *Fisheries Management and Ecology*, 21(6), pp.515–525.

Massa-Gallucci, A., Coscia, I., O'Grady, M., Kelly-Quinn, M. and Mariani, S., 2010. Patterns of genetic structuring in a brown trout (Salmo trutta L.) metapopulation. *Conservation Genetics*, 11(5), pp.1689–1699.

Matthews, M.A., Poole, W.R., Dillane, M.G. and Whelan, K.F., 1997. Juvenile recruitment and smolt output of brown trout (Salmo trutta L.) and Atlantic salmon (Salmo salar L.) from a lacustrine system in western Ireland. *Fisheries Research*, 31, pp.19–37.

Metcalfe, N.B., Fraser, N.H.C. and Burns, M.D., 1998. State-dependent shifts between nocturnal and diurnal activity in salmon. *Proceedings of the Royal Society B: Biological Sciences*, 265, pp.1503–1507.

Molloy, S., Holland, C. and O'Regan, M., 1995. Population biology of Pomphorhynchus laevis in brown trout from two lakes in the west of Ireland. *Journal of Helminthology*, 69, pp.229–235.

Morbey, Y., 2000. Protandry in Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, pp.1252–1257.

Morbey, Y.E., 2002. Protandry models and their application to salmon. *Behavioral Ecology*, 13(3), pp.337–343.

Morbey, Y.E. and Ydenberg, R.C., 2001. Protandrous arrival timing to breeding areas : a review. *Ecology Letters*, 4, pp.663–673.

Munro, M.A., Whitfield, P.J. and Diffley, R., 1989. Pomphorhynchus laevis (Muller) in the flounder , Platichthys flesus L ., in the tidal River Thames: population structure, microhabitat utilization and reproductive status in the field and under

conditions of controlled salinity. *Journal of Fish Biology*, 35, pp.719–735.

Nevoux, M., Finstad, B., Davidsen, J.G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O. and Jonsson, B., 2019. Environmental influences on life history strategies in partially anadromous brown trout (Salmo trutta, Salmonidae). *Fish and Fisheries*, 20(6), pp.1051–1082.

O'Mahony, E.M., Bradley, D.G., Kennedy, C.R. and Holland, C. V, 2004. Evidence for the hypothesis of strain formation in Pomphorhynchus laevis (Acanthocephala) : an investigation using mitochondrial DNA sequences. *Parasitology*, 129, pp.341–347.

O'Mahony, E.M.O., Kennedy, C.R. and Holland, C. V, 2004. Comparison of morphological characters in Irish and English populations of the acanthocephalan Pomphorhynchus laevis (Müller, 1776). *Systematic Parasitology*, (59), pp.147–157.

O'Toole, C.L., Reed, T.E., Bailie, D., Bradley, C., Cotter, D., Coughlan, J., Cross, T., Dillane, E., Mcevoy, S., Ó Maoiléidigh, N., Prodöhl, P., Rogan, G. and McGinnity, P., 2015. The signature of fine scale local adaptation in Atlantic salmon revealed from common garden experiments in nature. *Evolutionary Applications*, 8(9), pp.881–900.

Ovidio, M., Baras, E., Goffaux, D., Giroux, F. and Philippart, J.C., 2002. Seasonal variation of activity pattern of brown trout (Salmo trutta) in a small stream as determined by radio-telemetry. *Hydrobiologia*, 470, pp.195–202.

Palmé, A., Laikre, L. and Ryman, N., 2013. Monitoring reveals two genetically distinct brown trout populations remaining in stable sympatry over 20 years in tiny mountain lakes. *Conservation Genetics*, 14(4), pp.795–808.

Palmer, M.A. and Poff, N.L.R., 1997. Heterogeneity in streams: The influence of environmental heterogeneity on patterns and processes in streams. *Journal of the North American Benthological Society*, 16(1), pp.169–173.

Palmer, T.M., 2003. Spatial habitat heterogeneity influences competition and coexistence in an African acacia ant guild. *Ecology*, 84(11), pp.2843–2855.

Pettersen, R.A., Hytterød, S., Vøllestad, L.A. and Mo, T.A., 2013. Osmoregulatory disturbances in Atlantic salmon, Salmo salar L., caused by the monogenean Gyrodactylus salaris. *Journal of Fish Diseases*, 36(1), pp.67–70.

Poole, W.R., Dillane, M., Deeyto, E., Rogan, G., Mcginnity, P. and Whelan, K., 2007. Characteristics of the Burrishoole Sea Trout Population: Census, Marine Survival, Enhancement and Stock-Recruitment Relationship, 1971-2003. In: G. Harris and N. Milner, eds. *Sea Trout: Biology, Conservation and Management*. Wiley-Blackwell.pp.279–306.

Poole, W.R., Whelan, K.F., Dillane, M.G., Cooke, D.J. and Matthews, M., 1996. The performance of sea trout, Salmo trutta L., stocks from the Burrishoole system western Ireland, 1970-1994. *Fisheries Management and Ecology*, 3(1), pp.73–92.

Prentice, E.F., Flagg, T.A. and McCutcheon, C.S., 1990. Feasibility of Using Implantable Passive Integrated Transponder (PIT) Tags in Salmonids. *American Fisheries Society Symposium*, 7, pp.317–322.

Quéméré, E., Baglinière, J.L., Roussel, J.M., Evanno, G., McGinnity, P. and Launey, S., 2016. Seascape and its effect on migratory life-history strategy influences gene flow among coastal brown trout (Salmo trutta) populations in the English Channel. *Journal of Biogeography*, 43(3), pp.498–509.

Quinn, T.P. and Adams, D.J., 1996. Environmental changes affecting the migratory timing of american shad and sockeye salmon. *Ecology*, 77(4), pp.1151–1162.

Quinn, T.P., Unwin, M.J. and Kinnison, M.T., 2000. Evolution of temporal isolation in the wild: Genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution*, 54(4), pp.1372–1385.

Roohi, J.D., Pazooki, J. and Sattari, M., 2015. The first record of Pomphorhynchus laevis (Acanthocephala) in Chub, Squalius cephalus (Linnaeus, 1758) from Gamasiab River, Hamedan, Iran. *Caspian Journal of Environmental Science*, 13(2), pp.173–178.

Rustadbakken, A., L'Abee-Lund, J.H., Arnekleiv, J.V., Kraabøl, M., L'Abée-Lund, J.H., Arnekleiv, J.V. and Kraabøl, M., 2004. Reproductive migration of brown trout in a small Norwegian river studied by telemetry. *Journal of Fish Biology*, 64, pp.2–15.

Schindler, D.E., Armstrong, J.B. and Reed, T.E., 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, 13(5), pp.257–263.

Snyder, R.E. and Chesson, P., 2004. How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. *American Naturalist*, 164(5), pp.633–650.

Stein, A., Gerstner, K. and Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7), pp.866–880.

Stevens, R.D. and Tello, J.S., 2011. Diversity begets diversity: relative roles of

structural and resource heterogeneity in determining rodent community structure. *Journal of Mammalogy*, 92(2), pp.387–395.

Swadling, K.M., 2006. Krill Migration: Up and Down All Night. *Current Biology*, 16(5), pp.173–175.

Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H. and Finstad, B., 2012. A critical life stage of the Atlantic salmon Salmo salar: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81(2), pp.500–542.

Tully, O. and Whelan, K.F., 1993. Production of nauplii of Lepeophtheirus salmonis (Krøyer) (Copepoda: Caligidae) from farmed and wild salmon and its relation to the infestation of wild sea trout (Salmo trutta L.) off the west coast of Ireland in 1991. *Fisheries Research*, 17(1–2), pp.187–200.

Wanstall, S.T., 1984. *A study of the pathobiology of Pomphorhynchus laevis Muller in freshwater fish*. Derbyshire College of Further Education.

Wanstall, S.T., Robotham, P.W.J. and Thomas, J.S., 1986. Pathological changes induced by Pomphorbynchus laevis Muller (Acanthocephala) in the gut of rainbow trout, Salmo gairdneri Richardson. *Parasitenkunde*, 72, pp.105–114.

Wanstall, S.T., Thomas, J.S. and Robotham, P.W.J., 1988. The pathology caused by Pomphorhynchus laevis Muller in the alimentary tract of the stone loach, Noemacheilus harbatulus (L.). *Journal of Fish Diseases*, 11, pp.511–523.

Whelan, K., 2010. *A Review of the Impacts of the Salmon Louse, Lepeophtheirus salmonis (Krøyer, 1837) on Wild Salmonids*. *Atlantic Salmon Trust*, Perth.

Wilcove, D.S., 2008. *No Way Home: The Decline of the World's Great Animal*

Migrations. Washington: Island Press.

Zavorka, L., Aldven, D., Naslund, J., Hojesjo, J. and Jonsson, J.I., 2016. Inactive trout come out at night: behavioral variation, circadian activity, and fitness in the wild. *Ecology*, 97(9), pp.2223–2231.

Ziolkowska, M., Chibani, M., Kijewska, M. and Rokicki, J., 2000. The occurrence of Pomphorhynchus laevis (Muller, 1776) (Acanthocephala) and the age of the flounder (Platichthys flesus , L.). *Helminthology*, 37(3), pp.159–161.

Appendix A

The following figures and table are taken from an additional related branch of research I have been conducting in the Burrishoole catchment, using the PIT tag technology and installations described in the main body of my thesis, on the movement and survival of Atlantic salmon smolts through differing freshwater habitats in relation to environmental conditions. I intend to include a number of these figures in a paper that is currently in preparation for publication. The figures and table use a combination of long-term (1976 – 2019) smolt movement data collected from the Salmon Leap and Mill Race fish traps at the outflow of Lough Feeagh (sea entry end) and concurrent environmental data (Lough Feeagh surface water temperature and water height) as well as PIT-derived movement and survival data that I collected between 2017 and 2019. Between March and July in 2017, 2018 and 2019, 450 individual smolts that had been previously tagged upstream in the catchment were detected passing the Black River antenna, the Salmon Leap antenna or both.

Although the Black River antenna (Fig. 1) is located ~ 805 m upstream of Lough Feeagh, this section of the river is very slow moving and almost indistinguishable from lacustrine habitat during low flow periods. The mean time it takes for smolts to move from the Rough River trap to the Black River antenna (~ 3000 m) is 4.5 days, with most individuals taking significantly less time and a small number taking considerably longer (Fig. 2). As such, smolts moving downstream past the Black River antenna are deemed to be on the cusp of entering Lough Feeagh for the purpose of these analyses.

Fig. 3 shows that smolts entering Lough Feeagh early in the 2017 and 2018 smolt runs spent significantly longer in the lake than those that entered the lake later, possibly due to a period of low (i.e. < 0.24 m) water levels in April-May 2017 (Fig. 4. And Fig. 9) and lower than normal water temperatures in April-May 2018 (Fig. 5 and Fig. 9). In 2019, neither lake level or temperature were low during April-May (Fig. 9, temperature data not shown) and the lake transit duration was not correlated with entry date (Fig. 3). Fig. 6 is generated from a binary GLMM in which successful passage through Lough Feeagh is the binary response variable (Table 1). This figure and table show that the probability of successful passage through Lough Feeagh (i.e. through-lake-survival) was strongly positively correlated with entry date in 2017 and 2018, but not in 2019, which, in conjunction with Fig. 3, indicates that through-lake-mortality risk is associated with duration of lake transit (i.e. the longer that lake transit takes, the higher the mortality risk).

Fig 7. is generated from the binary GLMM outlined in Table 2 and shows the probability of the daily proportion of the annual smolt run out of Feeagh exceeding the long term mean proportion of the annual smolt run for that day number at five different lake surface temperature deviations from the long term mean temperature for that day number. Lake height is on the x axis and the underlying model was restricted to data from the days preceding the date on which 50 % of the smolt run exited the lake. This was done because, as the number of smolts upstream of sea entry drops, the opportunity for the daily proportion to exceed the long term proportion for that day number drops. This figure indicates that, although smolt movement is correlated with lake height, the likelihood of a higher proportion of smolts moving on a particular day number than the long term mean proportion for that day number is greatly reduced when the lake temperature is below average for

that day number. All underlying assumptions were met for the models presented in Table 1 and 2.

Fig. 8 shows the diel distribution of first detections of smolts (i.e. one per fish per antenna) at the Black River and Salmon Leap antennae, revealing that smolts primarily move through the Black River shortly after sunset while movements out of the lake are mostly diurnal and decrease substantially after sunset. Fig. 9 shows the number of smolts moving through the Rough River Trap and through the sea entry traps in 2017, 2018 and 2019 as well as concurrent lake surface temperatures and lake water levels.

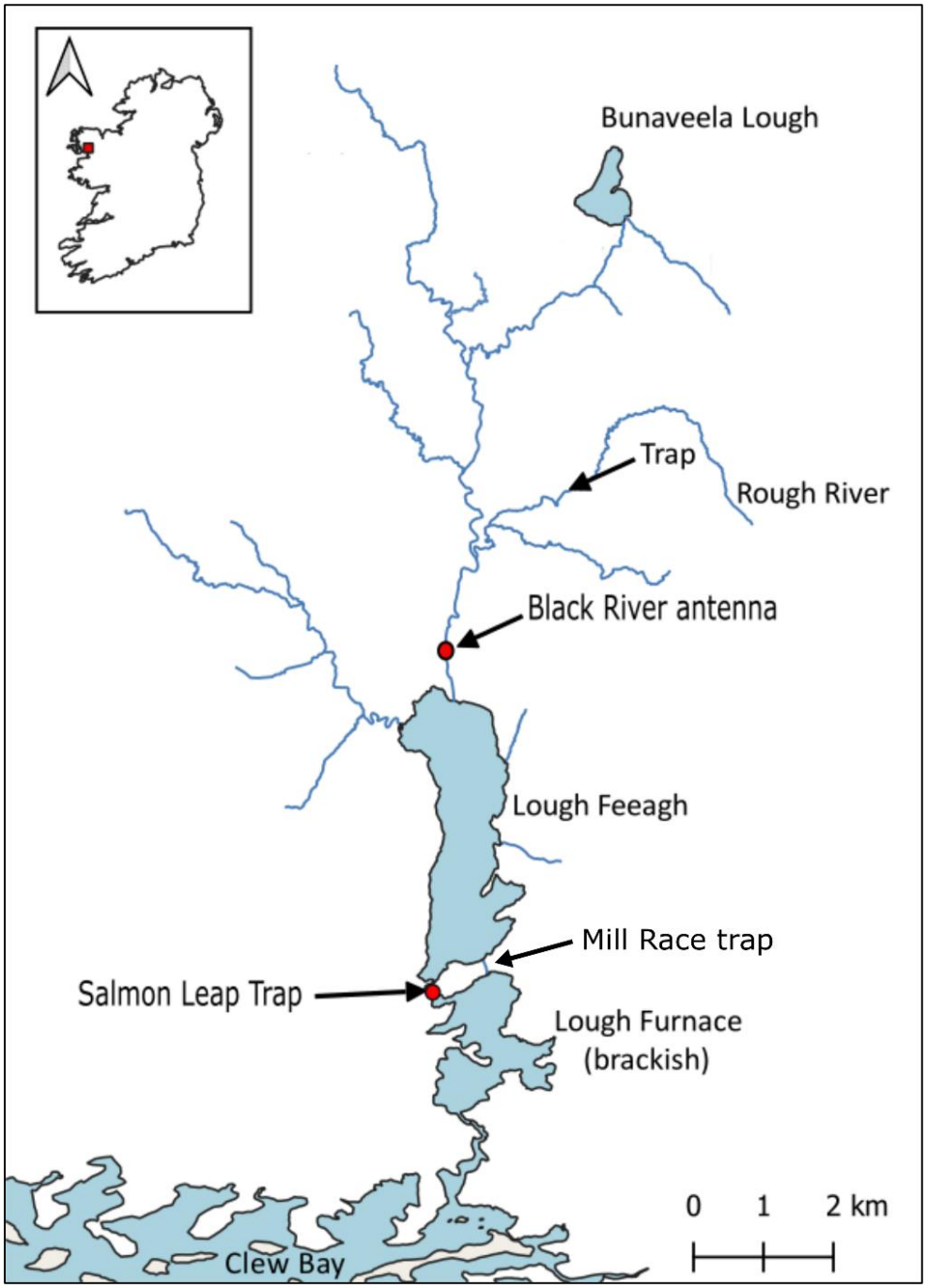


Figure 1. Map of the Burrishoole catchment showing the location of the Rough River fish trap, the Black River PIT antenna (red circle) and the PIT antenna at the Salmon Leap fish trap (red circle).

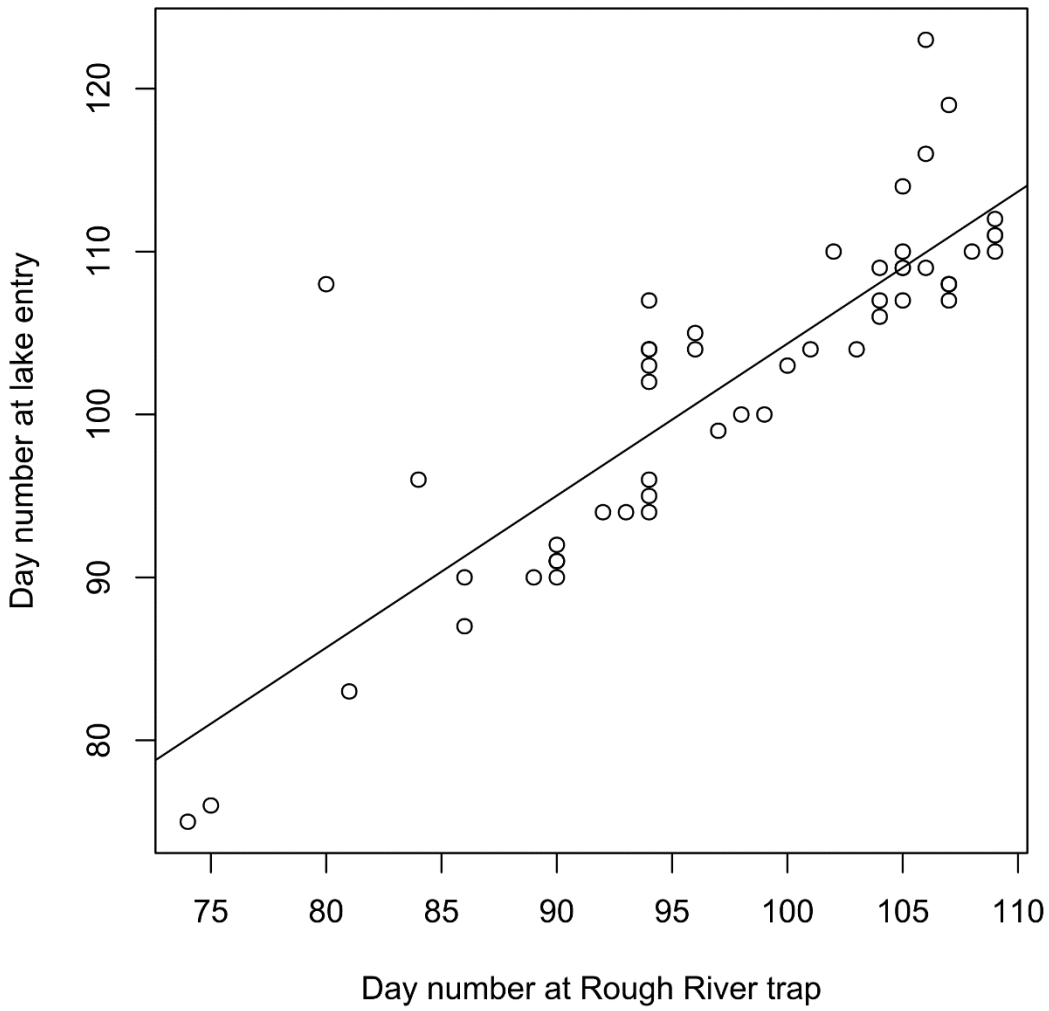


Figure 2. Day number that individual Atlantic salmon smolts were first detected by the Black River antenna (i.e. approaching lake entry) vs day number that the same smolts moved downstream through the Rough River trap. Mean time from the Rough River trap to the Black River antenna = 4.5 days. Data collection period: March – July 2017, 2018 and 2019.

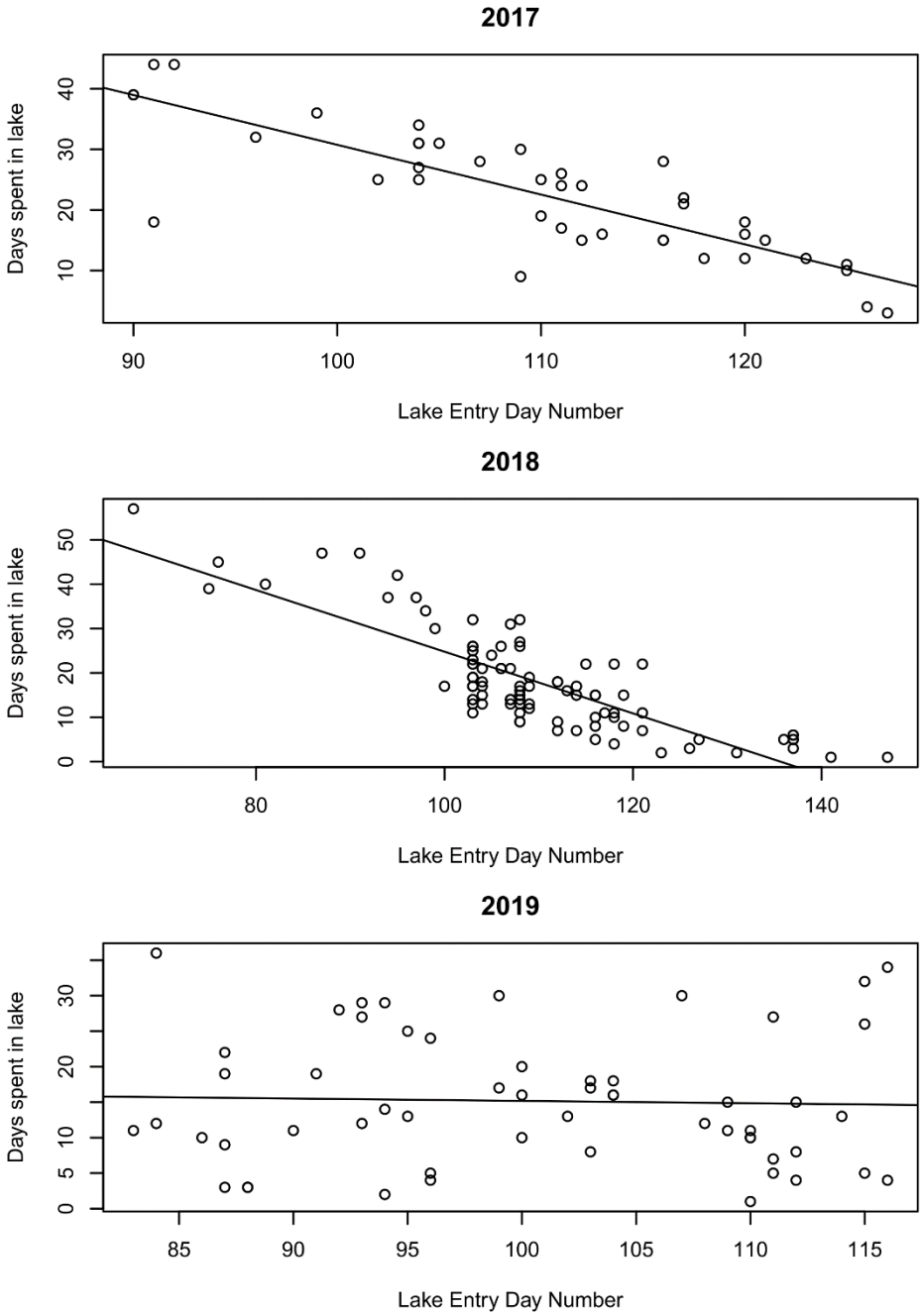


Figure 3. Number of days spent in Lough Feeagh vs the day number of lake entry for individual smolts detected in 2017, 2018 and 2019. Lake levels were low for much of the smolt run in 2017 (Fig. 4) Lake temperature was lower than long term mean temperatures in the first half of the smolt run in 2018 (Fig. 5). In 2019 there were no low water levels during the smolt run and water temperatures were slightly higher than long term mean temperatures (not shown).

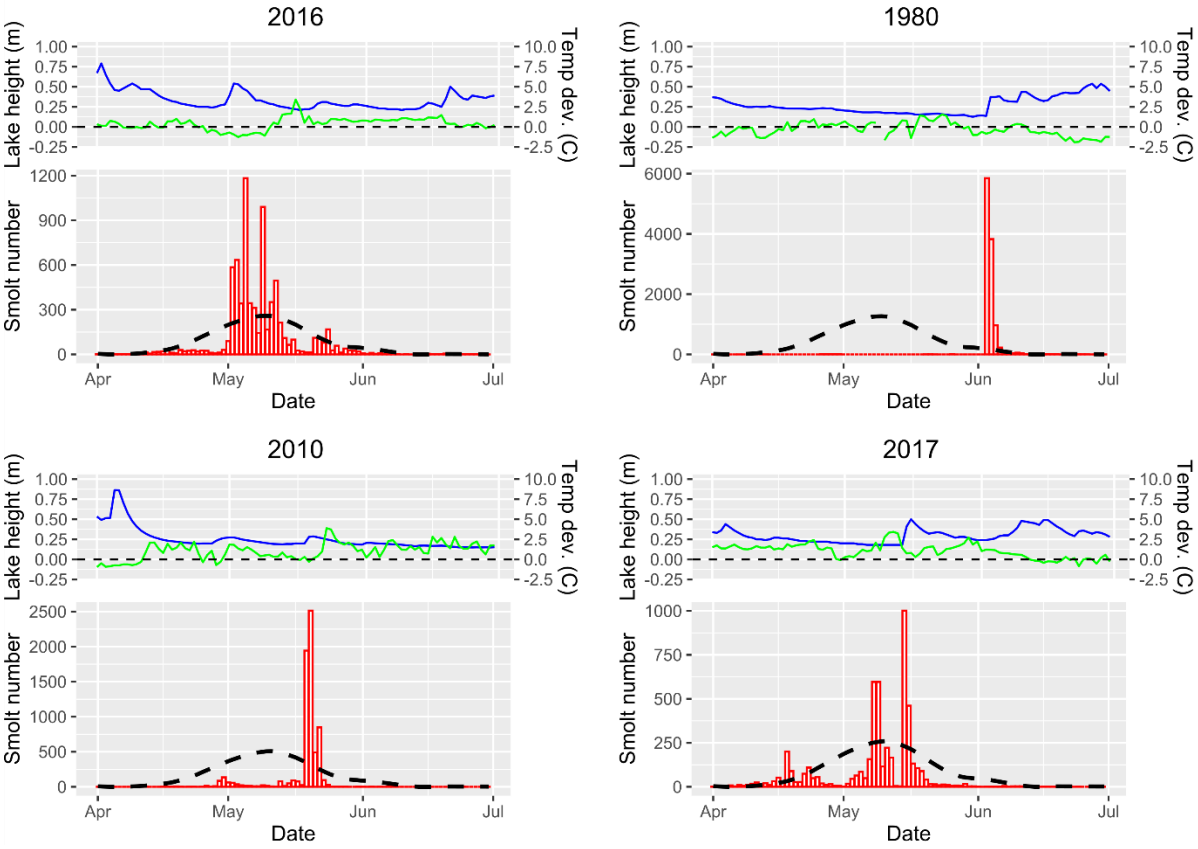


Figure 4. Red bars are the number of smolts that moved downstream out of Lough Feeagh per day. Black curved dashed lines represent the mean temporal distribution of the annual smolt run that moved downstream out Lough Feeagh over 43 years (1976 – 2019). Green lines represent the daily deviation (in °C) from the long-term (1976-2019) mean temperature for that day of the year. Blue lines represent water level (m) in Lough Feeagh. Straight black dashed lines designate the mean temperature for each day (i.e. when the green line is below this line the temperature is below average for that day of the year). Each year shown above experienced a period of drought (i.e. lake height < 0.25).

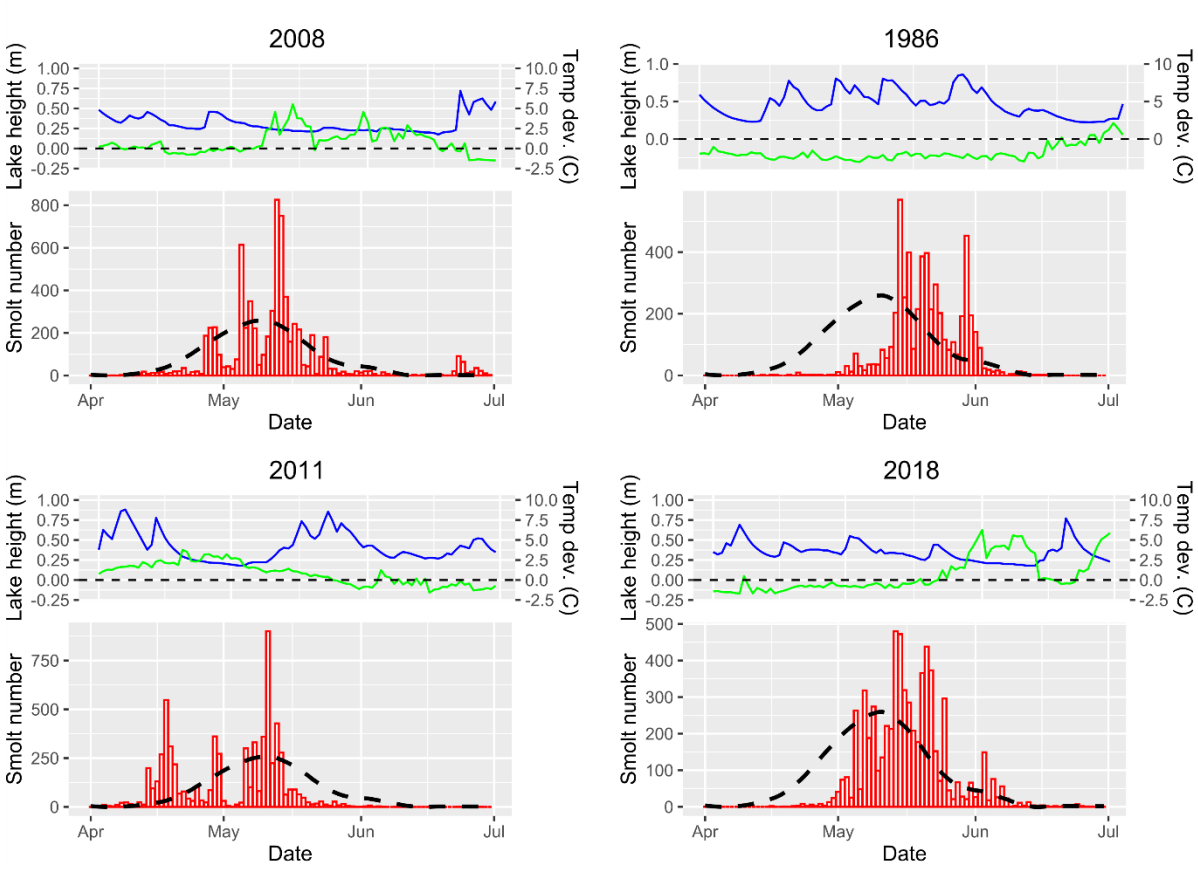


Figure 5. Red bars are the number of smolts that moved downstream out of Lough Feeagh per day. Black curved dashed lines represent the mean temporal distribution of the annual smolt run that moved downstream out Lough Feeagh over 43 years (1976 – 2019). Green lines represent the daily deviation (in °C) from the long-term (1976-2019) mean temperature for that day of the year. Blue lines represent water level (m) in Lough Feeagh. Straight black dashed lines designate the mean temperature for each day (i.e. when the green line is below this line the temperature is below average for that day of the year). 2011 represents a 'warm' year (i.e. warmer than the long term mean temperature through April and May), 1986 and 2018 represent 'cold' years and 2008 represents a 'normal' year.

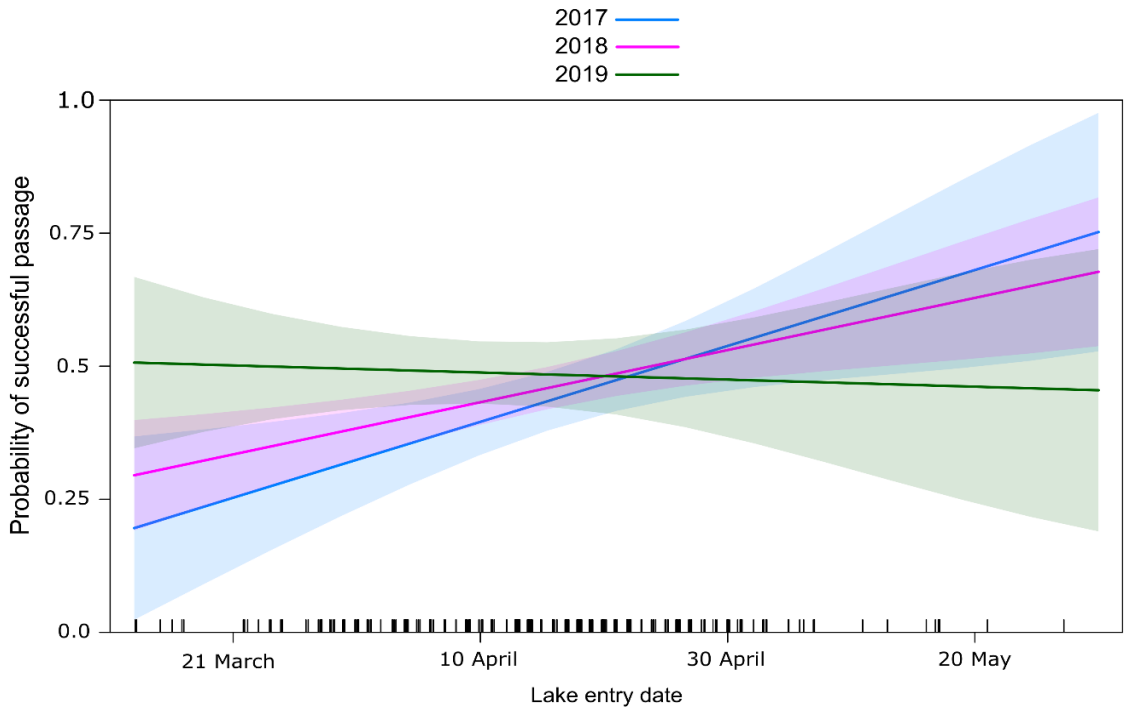


Figure 6. Probability of successful smolt passage through Lough Feeagh (i.e. survival) in relation to entry date for 2017, 2018 and 2019 as predicted from a binomial GLMM. Shaded areas represent the 95% confidence intervals.

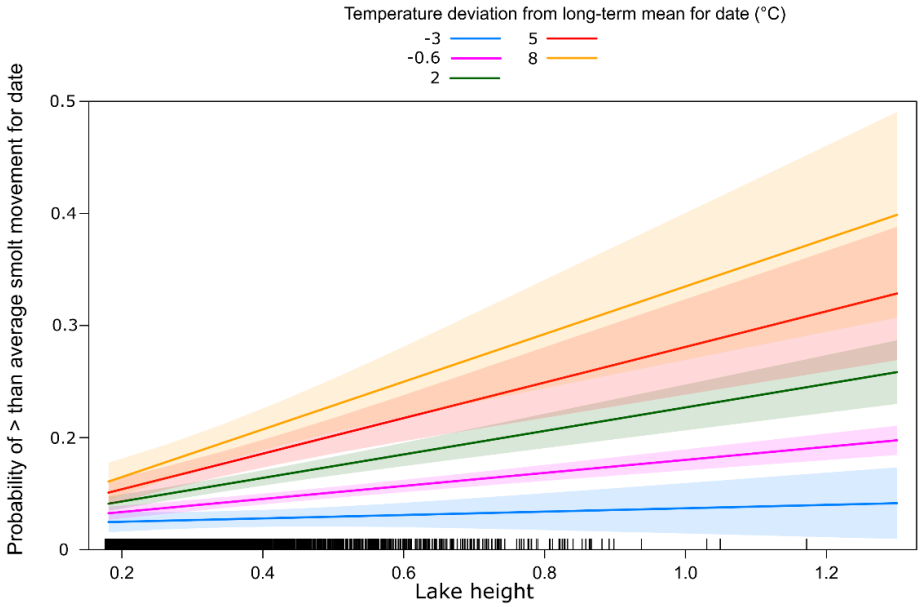


Figure 7. Probability that the daily proportion of the total annual number of smolts migrating downstream out of Lough Feeagh will exceed the long-term (1976-2019) mean proportion of the annual smolt run out of Lough Feeagh for that day number vs lake height (m) at five levels of water temperature deviation from the long-term mean temperature for that day number.

Table 1. Parameter estimates for the main effects and interaction effects from a binary GLMM, where successful passage through Lough Feeagh (i.e. survival) is the binary response variable. Data for model come from PIT detections at the Black River antenna and the Salmon Leap and Mill Race traps in 2017, 2018 and 2019. All estimates and their standard errors are on the logit scale and therefore correspond to log odds ratios. The odds ratio is also given (exponent of logit-scale parameter estimates), as well as the 5% and 95% confidence intervals around this. The intercept corresponds with 2017.

	Estimate	Std. Error	z value	Odds ratio	5% CI	95% CI	p value
(Intercept)	-7.178	2.696	-2.663	0.001	9.06-e06	0.064	0.008
Lake Entry Day Number	0.073	0.025	2.854	1.075	1.031	1.121	0.004
Year:2018	2.644	3.144	0.841	0.079	0.079	247.911	0.401
Year: 2019	8.876	3.879	2.288	7159.911	12.122	4227858.2	0.022
Lake entry day number × *Year 2018*	-0.023	0.030	-0.764	0.978	0.931	1.027	0.445
Lake entry day number × *Year 2019*	-0.079	0.037	-2.117	0.924	0.869	98.247	0.034

Table 2. Parameter estimates for the main effects and interaction effects from the binary GLMM, where the daily deviation direction from the long-term mean proportion of the smolt run out of Lough Feeagh for that day number (either above or below the mean) is the binary response variable. Data are restricted to the period of the smolt run prior to the date on which 50 % of the smolt run exited Lough Feeagh. All estimates and their standard errors are on the logit scale and therefore correspond to log odds ratios. The odds ratio is also given (exponent of logit-scale parameter estimates), as well as the 5% and 95% confidence intervals around this. The random effect *Year* has 43 levels corresponding with 1976-2019. Marginal R^2= 0.16, Conditional R^2= 0.43.

	Estimate	Std Error	z value	Odds ratio	5%	95%	p value
(Intercept)	-1.361	0.212	-6.409	0.256	0.181	0.364	<0.0001
Lake height	0.843	0.083	10.138	2.324	2.027	2.664	<0.0001
Temperature deviation	0.847	0.126	6.738	2.333	1.897	2.869	<0.0001
Lake height × *Temperature deviation*	0.349	0.106	3.284	1.417	1.190	1.688	0.001
Year (Random effect)				3.465	2.676	4.801	

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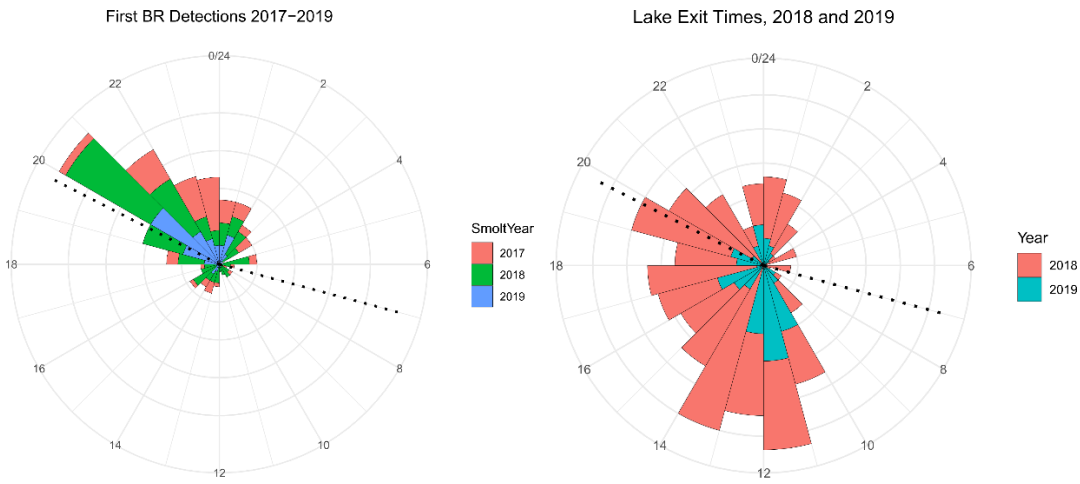


Figure 8. Diel timing of first Black River antenna detections (i.e. lake entry) for smolts detected in 2017, 2018 and 2019 and lake diel timing of first detections at the Salmon Leap trap antenna (i.e. lake exit) for smolts detected in 2018 and 2019.

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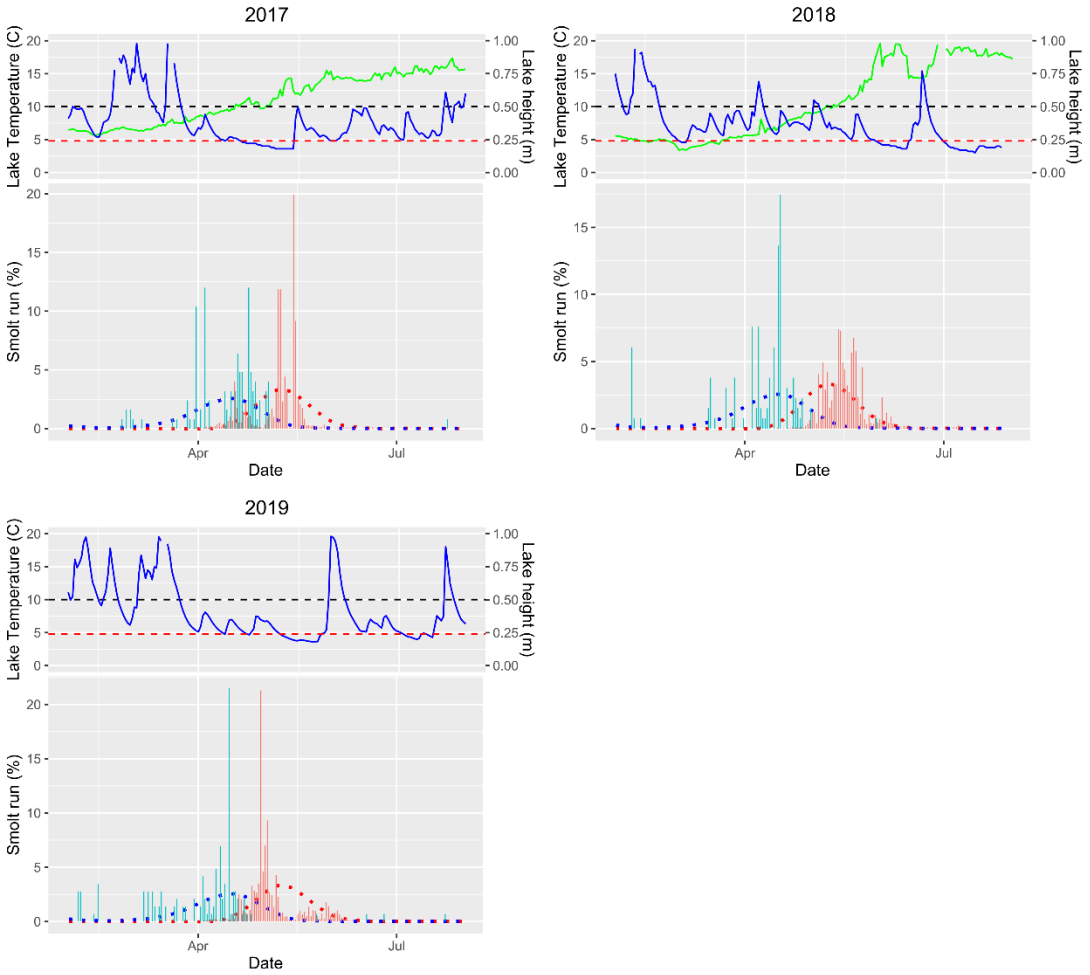


Figure 9. Blue bars are the daily percentage of the year's smolt run that moved downstream through the Rough River trap. Pink bars the daily percentage of the year's smolt run that moved downstream out of Lough Feeagh. Blue dotted lines represent the average distribution of annual smolt run that moved downstream through the Rough River trap over 11 years between 1994 and 2019. Red dotted lines represent the average distribution of annual smolt run that moved downstream out Lough Feeagh over 43 years (1976 – 2019). Green lines represent water surface temperature in Lough Feeagh. Blue lines represent water level in Lough Feeagh. Black dashed lines designate 10 °C. Red dashed lines designate a water level of 0.24 m (i.e. low lake level).

Appendix B

ICES Working Group with the Aim to Develop Assessment Models and Establish Biological Reference Points for Sea Trout (Anadromous *Salmo trutta*) Populations (WGTRUTTA).

Background

The working group was established in 2017. The inclusion of sea trout and other diadromous fish in EU policy areas including the CFP and Marine Strategy Framework Directive means that it is important to improve the methods currently available to managers to assess the status of stocks and investigate the effects of management actions.

The final report and recommendations will guide both individual countries in making progress on sea trout assessment and management and will steer ICES on the best next steps for sea trout science, assessment and advice. The Working Group addressed the following Terms of Reference:

a) Compile information from a selection of suitable rivers across Europe with long-term data on parameters such as juvenile densities, habitat characteristics and, if available, abundances of ascending spawners and out-migrating smolts

b) Develop new, validate and fine tune existing population models for sea trout

c) Establish and evaluate different approaches for estimating Biological Reference Points (BRPs) across regions with different characteristics and conditions for sea trout

Executive Summary of the Draft Final Report (2020)

The Working Group "WGTRUTTA" was established in 2017 with the Aim to Develop Assessment Models and Establish Biological Reference Points for Sea Trout (Anadromous *Salmo trutta*) Populations. The WG has representatives from every country containing a self-reproducing population of sea trout throughout Europe, in total 19 countries. Over the 3-year period, 31 experts were actively involved in the four workshops: Sweden (Gothenburg, 2017), Denmark (Copenhagen 2018), Portugal (Lisbon 2018) and UK (Dorchester 2019), as well as through intersessional activities.

Four subgroups worked to deliver the three ToR:

1 - Compile information from a selection of suitable rivers across Europe with long-term data on parameters such as juvenile densities, habitat characteristics and, if available, abundances of ascending spawners and out-migrating smolts;

2 - Develop new, validate and fine tune existing population models for sea trout;

3 - Establish and evaluate different approaches for estimating Biological Reference Points (BRPs) across regions with different characteristics and conditions for sea trout.

However, there is much that remains to be done to fully develop and implement the science of sea trout assessment and management, and to this end a resolution for a second 3-year term has been proposed.

The sea trout database structure was completed and populating it with data is well underway. This database is designed to provide a central depository for data used by the WG, and consists of two components: for environmental and bio-ecological data. The WG has created an inventory of data collection methods across the 19 countries of the natural range. There are common methodological approaches but few, if any, that are uniform across all countries. An inventory of PIT tagging infrastructure has also been created and will be made available via a mapping tool. The WG are liaising with ICES and their Regional Database and Estimation System (RDBES), working towards a time when ICES will host the WGTRUTTA database.

The WG undertook a comprehensive review of the scientific literature on ecological factors affecting the abundance and life history of anadromous fish which has been published in Fish and Fisheries (Nevoux et al., 2019), Appendix C. This provides the knowledge base to support development of population models, taking into account these complexities in the life history of the resident and anadromous components of stocks.

The WG has developed a set of length-based indicators to assess the status of a stock (after WKLIFE), using index catchments to demonstrate these indicators and to identify where pressures may have had an impact. Two papers, both published, have been developed describing the development and application of these length-based indicators of sea trout stock status (Shephard et al., 2019, 2018).

The WG has extended the development and application of the Trout Habitat Scores (THS) model using Baltic data from Sweden, and commenced testing this with data from Northern Ireland. A theoretical Bayesian Population Dynamics Model for Baltic sea trout is also being developed.

The challenges of developing and applying a BRP approach to sea trout were further explored by applying several curve fitting approaches (including Beverton-Holt, Ricker, Hockey Stick) to 'data rich' stocks with data from counts, returning stock estimates, catches, and juvenile abundance surveys. A 'one-size-fits-all' option is highly unlikely, but a suite of tools is more promising, especially if they can be targeted towards a relatively small number of sea trout stock groupings. A grouping proposed for 16 sea trout stocks in England and Wales, based on growth rates and longevity, has been identified as a potential stock grouping tool and it is proposed to test and develop this across the natural range of the species in future research. Such groupings might be used as the basis for focussing stock-recruitment or other model approaches, and/or to make recommendations on selecting index rivers and data collection programs.

The WG developed a Resolution for a second 3-year term, and a proposal for a nested series of PhDs to broaden the delivery and dissemination of the WG activities which was submitted to the Marie Skłodowska-Curie actions to support Innovative Training Networks (ITNs) at the end of 2019.

References

Nevoux, M., Finstad, B., Davidsen, J.G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O. and Jonsson, B., 2019. Environmental

influences on life history strategies in partially anadromous brown trout (Salmo trutta, Salmonidae). *Fish and Fisheries*, 20(6), pp.1051–1082.

Shephard, S., Josset, Q., Davidson, I., Kennedy, R., Magnusson, K., Gargan, P.G., Walker, A.M. and Poole, R., 2019. Combining empirical indicators and expert knowledge for surveillance of data-limited sea trout stocks. *Ecological Indicators*, 104, pp.96–106.

Shephard, S., Roche, W.K., Ryan, D., Shephard, S., Gargan, P. and Roche, W., 2018. Estimating sea trout (Salmo trutta L .) growth from scale chemistry profiles : an objective approach using LA-ICPMS Estimating sea trout (Salmo trutta L .) growth from scale chemistry pro fi les : an objective approach using LA-ICPMS. *Fisheries Research*, 211, pp.69–80.

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ORIGINAL ARTICLE

FISH and FISHERIES WILEY

Environmental influences of life history strategies in partial anadromous brown trout (*Salmo trutta*, Salmonidae)

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Abstract

This paper reviews the life history of brown trout and factors influencing decisions to migrate. Decisions that maximize fitness appear dependent on size at age. In partly anadromous populations, individuals that attain maturity at the parr stage typically become freshwater resident. For individual fish, the life history is not genetically fixed and can be modified by the previous growth history and energetic state in early life. This phenotypic plasticity may be influenced by epigenetic modifications of the genome. Thus, factors influencing survival and growth determine life-history decisions. These are intra- and interspecific competition, feeding and shelter opportunities in freshwater and salt water, temperature in alternative habitats and flow conditions in running water. Male trout exhibit alternative mating strategies and can spawn as a subordinate sneaker or a dominant competitor. Females do not exhibit alternative mating behaviour. The relationship between growth, size and reproductive success differs between sexes in that females exhibit a higher tendency to migrate than males. Southern populations are sensitive to global warming. In addition, fisheries, aquaculture with increased spreading of salmon lice, introduction of new species, weirs and river regulation, poor water quality and coastal developments all threaten trout populations. The paper summarizes life-history data from six populations across Europe and ends by presenting new research questions and directions for future research.

KEYWORDS

freshwater resident, habitat, migration, partial anadromy, Salmonidae, sex ratio

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1 | INTRODUCTION

Brown trout is a facultative (i.e. partly) anadromous species (Lobón-Cerviá, Rasmussen, & Mortensen, 2017). It typically spawns in freshwater, but may reproduce successfully in estuaries at salinities below 4 ppt, such as on the coast of Gotland in the Baltic Sea (Landergren & Vallin, 1998; Limburg, Landergren, Westin, Elfman, & Kristiansson, 2001). The species is partly migratory as some individuals within a population may reside in or near the spawning area all year round, whereas other individuals move out of this area for feeding. Migratory trout can be anadromous, feeding in the marine habitat. Migrants generally return to breed with high precision to their area of origin for spawning, but exceptions occur (Jonsson, Jonsson, & Jonsson, 2018).

Brown trout are phenotypically variable. Adult body length varies from approximately 10 to 100 cm (Evangelista, Boiche, Lecerf, & Cucherousset, 2014; Jonsson & Jonsson, 2011; Sánchez-Hernández, Eloranta, Finstad, & Amundsen, 2017). The species exploit habitats ranging from small brooks to rivers, lakes, estuaries and coastal sea, but are seldom found in the open ocean, though recent literature indicates that some brown trout may live a more pelagic life while at sea (Jonsson & Jonsson, 2011; Kristensen, Righton, del Villar-Guerra, Baktoft, & Aarestrup, 2018). Populations adapt trophically to and vary ecologically, morphologically, behaviourally and genetically with local conditions over the distribution area. This diversity complicates the systematics of the species and makes some scientists term *Salmo trutta* a species complex rather than a single species (Keller, Taverna, & Seehausen, 2011; Patarnello, Bargelloni, Caldara, & Colombo, 1994; Sanz, 2017). Although the systematics of brown trout have still to be resolved, the phylogeographic and the genetic structure of the species were recently clarified (Sanz, 2017).

Freshwater-resident populations are well described (Baglinière & Maisse, 2002; Frost & Brown, 1967; Gosset, Rives, & Labonne, 2006; Jonsson, 1989; Maisse & Baglinière, 1990). More complex is the ecology of anadromous trout (Harris, 2017; Harris & Milner, 2007), which occur naturally along the length of the Atlantic coast of Europe from northern Russia to Portugal, Iceland included, and occur as an introduced fish in North and South America, Australia, New Zealand and Kerguelen Islands (Baglinière, 1999; Elliott, 1994; Jonsson & Jonsson, 2011; Lecomte, Beall, Chat, Davaine, & Gaudin, 2013; Figure 1). The species is present along the coast of the Black and Caspian-Aral Seas in central Europe (Baglinière, 1999; Elliott, 1994; Jonsson & Jonsson, 2011). Among all introduced Salmonidae species, brown trout is the species with the highest success rate of naturalization and the largest distribution out of its original range. This is likely the result of a high adaptive capacity and tolerance for habitat change (Baglinière, 1999).

Brown trout have been the focus of several books such as those by Fahy (1985), Elliott (1994), Baglinière and Maisse (1999), Harris and Milner (2007), Harris (2017), Jonsson and Jonsson (2011), and Lobón-Cerviá and Sanz (2017). However, some recent knowledge on migration, its complexity and plasticity is not included in these books (Figure 2). This review is also motivated by the desire to complement the literature review with a compilation of data from six populations across Europe. Partly anadromous means that individual populations can consist of both freshwater resident and anadromous individuals. In this review, we present information on both these life-history components and discuss drivers of anadromy, the influence of the marine environment on the migration, and effects of spawning habitat on body size and sexual size dimorphism. Furthermore, we summarize knowledge on effects of interspecific competitors and predators on abundance and behaviour of brown trout and impacts of the parasitic sea lice on local sea trout, which constitutes one of the main threats to wild populations in some areas (Thorstad et al., 2015), and which has led to significant population collapses (e.g. Gargan, Poole, & Forde, 2006). Environmental constraints in freshwater may stimulate migration of brown trout, including constraints from competition, poor feeding and low growth opportunities. We review the effects of these, as well as negative environmental impacts at sea that may select against the propensity to migrate (Poole et al., 2007). Last, we present important questions for further research.

2 | RESIDENT VERSUS ANADROMOUS BROWN TROUT

2.1 | Historical overview

Carolus Linnaeus, in his 10th edition of Systema Naturae (1758), classified anadromous (sea) trout (*Salmo eriox*) as a different species from river trout (*Salmo trutta*). The classification was based on colouration and body form, a taxonomic classification maintained into the 19th century (Jonsson & Jonsson, 2011). Among others, Dahl (1904) questioned the classification as he observed that river trout could move downstream to sea. Furthermore, Regan (1911) proposed that anadromous and nonanadromous trout could be freely



FIGURE 1 Endemic distribution of brown trout: dashed lines give distribution area of anadromous populations, and shaded areas give those of freshwater-resident populations. After Jonsson and Jonsson (2011). Localization of six brown trout populations, from north to south: River Hals 70°N (Norway), River Vosso 60°N (Norway), River Burrishoole 54°N (Ireland), River Tamar 51°N (England), River Bresle 50°N (France) and River Oir 48°N (France)

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interbreeding fractions of a single species. Nevertheless, until the development of modern genetic techniques in the 1980s, much uncertainty remained about whether or not sea trout and river trout were the same or separate species (Frost & Brown, 1967).

2.2 | Two phenotypes and a single species

Brown trout may have split from Atlantic salmon (*Salmo salar*, Salmonidae) between 10 and 14 million years ago (Crête-Lafrenière, Weir, & Bernatchez, 2012), and the five major evolutionary lineages of brown trout evolved in its native Eurasian and North African range of distribution with geographic isolation occurring during the Pleistocene Ice Ages and have largely remained allopatric since then (Bernatchez, 2001). Their evolutionary histories have been shaped by glaciations, habitat loss and varying potential for dispersal. They survived in ice-free refuges during the periods of glaciation and colonized rivers as the ice cover retreated (McKeown, Hynes, Duguid, Ferguson, & Prodöhl, 2010). After the last glaciation period some 14,000 years ago, they entered rivers in the former glaciated northern areas and gradually acquired their natural area we see today (Ferguson, 2006). The anadromous behaviour probably existed before speciation of the salmonid family and the anadromous types, mainly of the genus *Salmo*, evolved from the freshwater forms (Balon, 1980).

By origin, brown trout is chiefly a European species, but populations have been introduced to areas outside their natural range they were unable to reach naturally (Jonsson & Jonsson, 2011). For instance, offspring of anadromous trout were released in some North American rivers, and from these progenitors, both anadromous and nonanadromous trout developed (Rounsefell, 1958), proving that the two trout forms could develop from single gene pools. Similar evidence was obtained from releases in the Kerguelen Islands (Davaine & Beall, 1997). The close connection between the two phenotypes was further highlighted by the observation that offspring of a population of resident mountain living brown trout feed and grow well at sea when transferred to a coastal river with free access to and from the sea (Jonsson, Jonsson, & Hansen, 1994). They also survive and grow when they are released directly into sea water as unsmoltified parr or immature brown

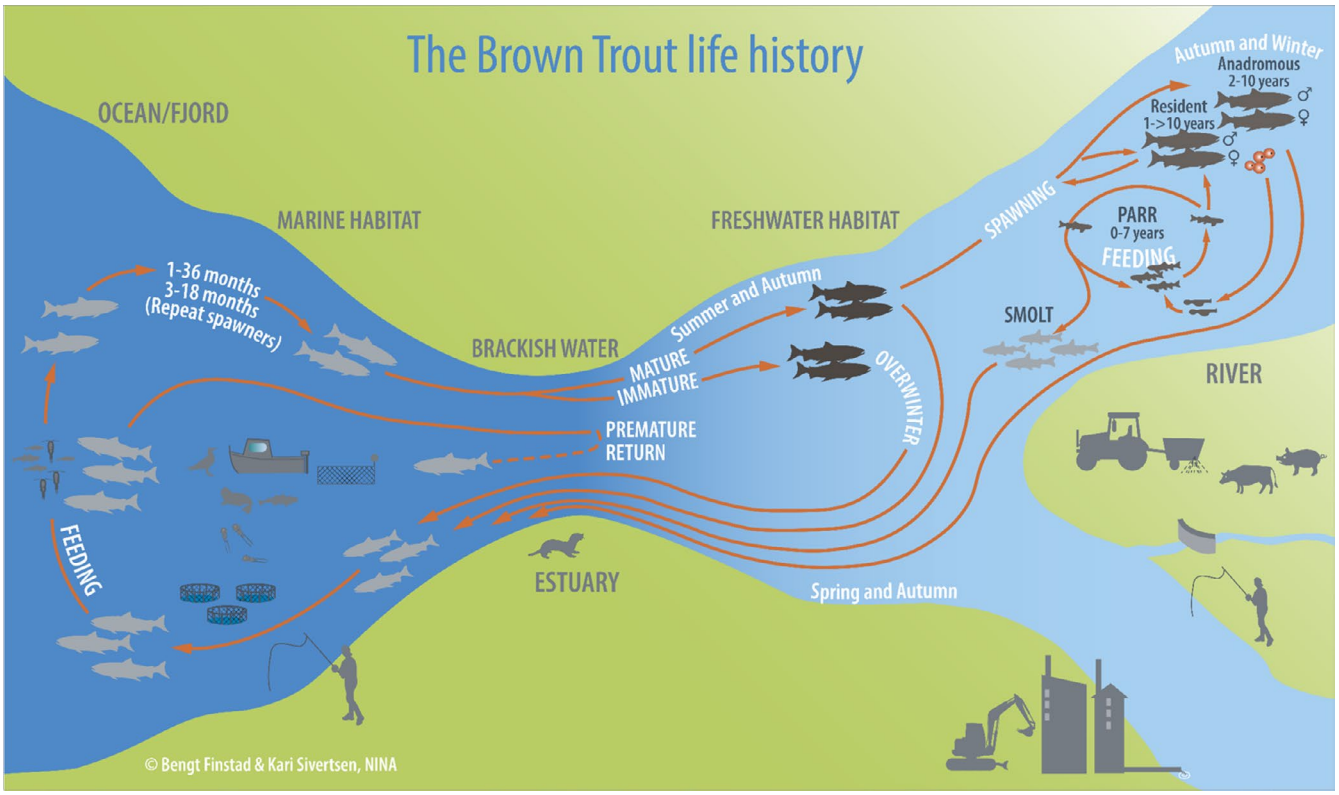


FIGURE 2 Schematic representation of brown trout life history, and some of the major threats affecting its abundance (© Bengt Finstad and Kari Sivertsen, NINA). Figure appears in colour in the online version only

trout (Jonsson, Jonsson, Hansen, & Aass, 1994), although osmoregulatory performance is favoured by a progressive transfer to seawater (Boeuf & Harache, 1982). Experimentally, Skrochowska (1969) and Ombredane, Siegler, Baglinière, and Prunet (1996) demonstrated that anadromous and nonanadromous parents produced both freshwater resident and sea-run migratory offspring. However, the proportion of anadromous offspring was higher for anadromous than nonanadromous parents, indicating a difference in gene expression between the two forms. Also, within single river systems, anadromous and nonanadromous trout spawn together as have been observed in the field (Charles, Guyomard, Hoyheim, Ombredane, & Baglinière, 2005; Cucherousset, Ombredane, Charles, Marchand, & Baglinière, 2005; Jonsson, 1985; Vøllestad, 2017), but the proportions of anadromous versus resident maternal origin parr will probably differ in different sections of the stream (Rohtla et al., 2017). Population diversification through anadromous and nonanadromous individuals is not unique to brown trout, but is also found in other salmonids (e.g. rainbow trout; *Oncorhynchus mykiss*, Salmonidae; Arctic charr; *Salvelinus alpinus*, Salmonidae) and some nonsalmonid species (e.g. American shad; *Alosa sapidissima*, Clupeidae; Jonsson & Jonsson, 1993).

2.3 | Contrast in gene expression

Although anadromous and nonanadromous trout are genetically similar when in sympatry (Charles et al., 2005; Cross, Mills, & Courcy Williams, 1992; Hindar, Jonsson, Ryman, & Ståhl, 1991; Pettersson, Hansen, & Bohlin, 2001), around 50% of the variability in migration versus residency among individuals within a population, may be due to genetic variance (Ferguson, Reed, Cross, McGinnity, & Prodöhl, 2019). Recent evidence suggests differences in the gene expression influencing the life history of the two trout phenotypes (Giger et al., 2006; Lemopoulos et al., 2018, 2017). For instance, Giger et al. (2006) demonstrated that the gene expression was primarily related to the migratory trait and not to genetic relatedness, whether the fish migrate to the sea or a lake. They found that migrant and freshwater-resident brown trout from the same area exhibited different gene expression profiles, whereas evolutionarily or geographically distant populations sharing the same life histories showed similar gene expression, that is similar levels of mRNA transcripts. For example, a resident population belonging to a Mediterranean lineage that diverged more than 500,000 years ago from the Atlantic lineage exhibited a gene expression profile like that of resident Atlantic populations. By contrast, migratory and resident trout from the same river had very different profiles (sets of mRNAs). Migration destination (mainstream river, lake or sea) also appears to be genetically programmed (Ferguson et al., 2019). Giger et al. (2006) suggested that the genetic difference between life-history types of brown trout is the result of a few controlling genes that determine the expression of many other genes defining the life-history pattern. They found that life-history differences explained 45% of the total variability

in gene expression levels, three times more than the variability explained by genetic diversity between populations. Thus, gene expression appears to be influenced by the environment and interactions between genes and environment that drive life history and migration decisions.

2.4 | Phenotypic plasticity

There is considerable variation in life-history strategies among individuals and populations, and in the timing and duration of marine migrations of brown trout (Aldvén & Davidsen, 2017; Jonsson, 1989; Thorstad et al., 2016). Figure 2 illustrates this diversity: after 1–7 years in freshwater, some individuals make a physiological transformation from parr to smolt and migrate to sea. Young parr may also make excursions into brackish water. Downstream migration usually takes place in spring and autumn (Aarestrup, Birnie Gauvin, & Larsen, 2017; Poole et al., 2007; Winter, Tummers, Aarestrup, Baktoft, & Lucas, 2016). Anadromous trout spend from 1 up to 36 months at sea on their maiden sea sojourn. In the marine habitat, they feed on polychaetes, crustaceans and small fish (Knutsen, Knutsen, Gjøsæter, & Jonsson, 2001), and grow more than in freshwater. Sometimes, anadromous trout perform an early (premature) return, characterized by a brief incursion in brackish or fresh water, before heading back to the sea; this phenomenon may be exacerbated by sea louse infestation (Birkeland, 1996). In summer, autumn and even winter, mature anadromous trout return to their natal river to breed. While immature anadromous trout from northern Europe may spend the winter in brackish or freshwater (often not in their natal river) before moving back to the sea in the following spring (Thomsen, Koed, Nielsen, & Madsen, 2007). Mature trout spawn in freshwater in the autumn/winter and return to sea immediately after spawning (Jonsson & Jonsson, 2009b, 2002) or in the subsequent spring (Jonsson, 1985). The former is more dominating for trout spawning in small water courses with poor shelter for wintering trout (Jonsson, Jonsson, Brodtkorb, & Ingebrigtsen, 2001; Jonsson, Jonsson, & Jonsson, 2018). Survivors typically undertake a shorter sea sojourn before heading back to freshwater as repeat spawners (Jonsson & Jonsson, 2009b). Some of the parr do not smolt and remain in freshwater during their entire life. Resident and anadromous trout can reproduce on sympatric spawning grounds, or spawn in separate areas of the same river (Hindar et al., 1991; Rohtla et al., 2017).

Brown trout exhibit a large range of body sizes across their endemic distribution range, with resident trout being on average smaller that anadromous trout (Figure 3). Within a given catchment, resident trout rarely become as large as their anadromous counterparts of similar age. However, older resident trout may become larger than young anadromous trout and the largest resident trout can be larger than the smallest anadromous specimen within age-classes (i.e. total age from birth). Large resident trout feeding on fish can grow equally large or larger than anadromous trout do. Ferox trout from Scottish and Irish Lochs are examples of such large resident trout (Campbell, 1979; Hughes et al., 2019).

The parameters controlling juvenile growth rate play an important role, and various thresholds regulate the individual's decision of life history and migration strategy. Growth rate variation induces two antagonistic phenomena: sexual maturation and migration (Baglinière & Maisse, 1985; Jonsson & Jonsson, 1993; Maisse & Baglinière, 1999). The higher the growth rate, the earlier the onset of maturation or migration. Presumably, the developmental threshold for precocious sexual maturation appears earlier in the

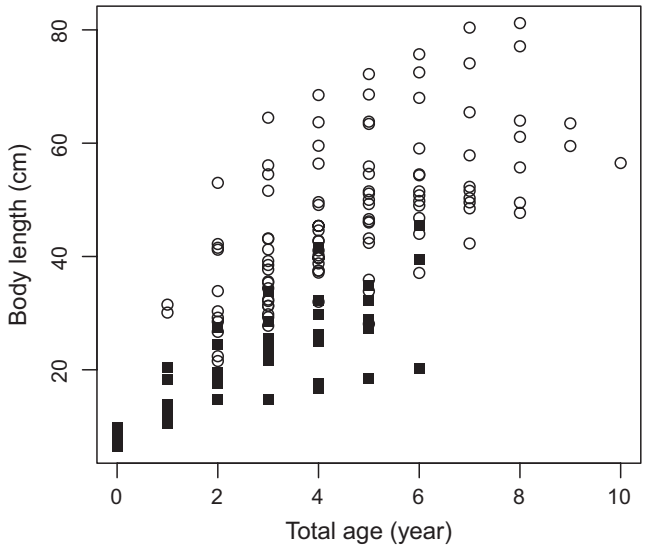


FIGURE 3 Mean length at age for resident (filled square) and anadromous (open dot) brown trout combined for the River Hals, River Vosso, River Tamar, River Bresle and River Oir. The total age represents the freshwater age for resident trout and the sum of the freshwater age and the sea age for anadromous. See Table S1 for details

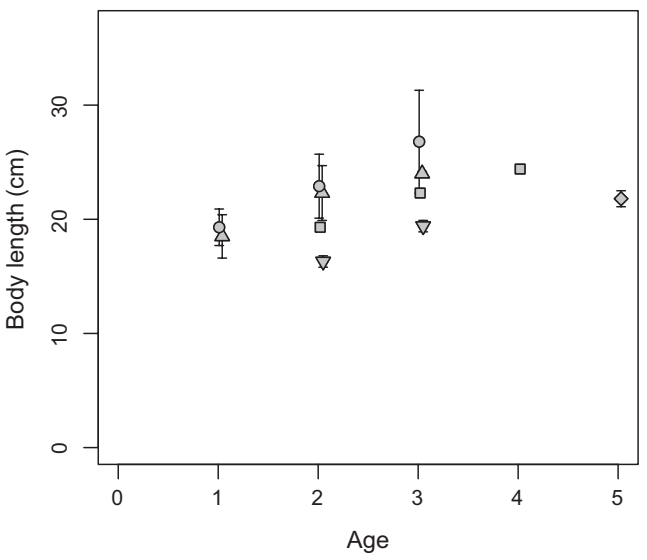


FIGURE 4 Mean length at age for brown trout smolts at River Hals (diamond), River Vosso (triangles point down), River Burrishoole (squares), River Bresle (dots) and River Oir (triangles point up). Values are presented ± 1 *SD*, except for River Burrishoole. See Table S1 for details

season than that for migration. In partly anadromous populations, mature parr typically become freshwater resident, although a few of them may migrate to sea in a later year (Jonsson & Jonsson, 2011). The characteristics of these thresholds, relative to the life stage of the fish, depend on environmental factors, the stage and sex of the trout, and its genotype (Baglinière, Guyomard, Héland, Ombredane, & Prévost, 2001). Across its European distribution area, the age of smolt vary widely, from 1–3 years in France to 5–7 years in northern Norway (Figure 4). Within each population, the size of smolts increases with age. This large-scale pattern suggests that despite phenotypic plasticity and local environmental constraints, a physiological threshold may underlie smolt migration in brown trout. We may add, however, that smolt size is particularly small among trout spawning in small streams, with some smolts as small as 8 cm being recorded (Jonsson et al., 2001).

Like in the Atlantic salmon, the parr–smolt transformation takes place in the largest juvenile trout of a given population (Tanguy, Ombredane, Baglinière, & Prunet, 1994) and smolting occurs in spring. Silvering encompasses a peak of gill Na^+/K^+-ATPase activity and a simultaneous decrease in plasma prolactin is observed, together with morphological changes (Aarestrup, Nielsen, & Madsen, 2000; Boeuf & Harache, 1982). But, compared to the Atlantic salmon, no surge in growth hormone is documented (Tanguy et al., 1994). Hypoosmoregulatory ability is greatest at the time of peak gill Na^+/K^+-ATPase activity, and it increases in spring in all trout, irrespective of smolt status (Nielsen, Aarestrup, & Madsen, 2006). Smolting appears less stringent in brown trout than in Atlantic salmon and does not seem to be an obligatory process for seawater adaptation in this species. The level of smolting also depends on stock origin and body size; for example, fast-growing juveniles can migrate to sea without smolting (Tanguy et al., 1994). Usually, juvenile trout migrate from rivers in spring (March–June in Europe; Byrne, Poole, Dillane, Rogan, & Whelan, 2004; Flaten et al., 2016; Jensen et al., 2012), but may also migrate at other times of the year, for example during autumn (Aarestrup et al., 2017; Jonsson & Jonsson, 2009a, 2002; Jonsson et al., 2018; Poole et al., 2007; Poole, Whelan, Dillane, Cooke, & Matthews, 1996; Taal et al., 2014; Winter et al., 2016), indicating that the time of seaward migration is highly plastic. There are indications that smolt run timing may be changing with migrations occurring earlier in recent years (Byrne et al., 2004), a phenomenon also observed in Atlantic salmon (Jonsson, Jonsson, & Finstad, 2014; Otero et al., 2014), possibly caused by climate change.

Post-smolt brown trout feed at sea and some immature fish return to estuaries or freshwater to overwinter, whereas others remain at sea (Jonsson et al., 2001, 2018). Evidence of unsmoltified parr making brief brackish water excursions to switch streams has also been documented (Taal et al., 2018). In northern Europe, immature trout can also return to freshwater in summer after a short stay at sea. Ionoregulation in sea water at low temperature is arduous, but anadromous trout have been observed at sea during winter and tolerate full salinity seawater at temperatures as low as 1–2°C (Eldøy et al., 2017; Jensen & Rikardsen, 2012; Knudsen et al., 2009; Olsen, Knutsen, Simonsen, Jonsson, & Knutsen, 2006). In the brackish Baltic Sea, parr can migrate from freshwater to the Baltic coastal zone without undergoing smolting. There, they may experience little or no physiological cost in terms of lower survival and growth from this transition (Landergren, 2005). Otoliths collected from brown trout in the Baltic Sea sometimes show no evidence of a freshwater history, raising the possibility of a contingent of the coastal population that does not depend on riverine spawning or that the fish move to sea as fry (Limburg et al., 2001). The duration and timing of marine migrations are likely governed by trade-offs between mortality risk and growth opportunities in different habitats, and the most beneficial strategy may vary among individuals and populations. Based on life table analysis, Jonsson (1981) found that the product of survival and fecundity, as a measure of fitness, was similar for freshwater resident and anadromous brown trout of the same population. Possibly, the fitness of different aged smolts is also similar as indicated from calculations of survival and fecundity of female Atlantic salmon (Jonsson, Jonsson, & Albretsen, 2016).

2.5 | Epigenetics

Divergent life-history phenotypes may be the result of epigenetic modifications that link environmental factors and the genome to regulate internal cues as reported from studies on steelhead trout (the anadromous form of the rainbow trout; Baerwald et al., 2016). The most studied epigenetic effect is a consequence of DNA methylation. High methylation levels are associated with silencing of gene expression, and demethylation is linked to active gene transcription (Bird, 2002). Evidence of an epigenetic effect on life-history variation was reported by Moran and Pérez-Figueroa (2011). They found a link between DNA methylation and maturation in Atlantic salmon male parr. Mature male parr exhibit reduced probability of smolting in brown trout (Jonsson, 1985) and Atlantic salmon (Berglund, 1995). Epigenetic effects can be mediated early, such as at the embryonic stage (Jonsson & Jonsson, 2019). For instance, thermal conditions during the embryogenesis may influence later growth, as found in Atlantic salmon (Finstad & Jonsson, 2012) and zebra fish (Scott & Johnston, 2012). Furthermore, there is evidence of multiple differentially methylated genes between anadromous and nonanadromous rainbow trout (Baerwald et al., 2016). They reported that smolting of steelhead trout is associated with DNA methylation pattern. Furthermore, it has been shown that salt-induced alterations in DNA methylation patterns play a role in sea water adaptation in fishes (Artemov et al., 2017; Moran, Marco-Rius, Megías, Covelo-Soto, & Pérez-Figueroa, 2013). One may hypothesize that early environmental factors may also influence life-history decisions and phenotypic plasticity in brown trout, although this has not yet been investigated.

3 | TRADE-OFFS BETWEEN GROWTH AND SURVIVAL

3.1 | Habitat selection theory

Mobile organisms are expected to select the most profitable feeding habitat. They should choose the habitat where mortality (μ)

over growth (g) (μ/g) is minimized (Werner & Gilliam, 1984). These two components are main determinants of their fitness. The relative value of feeding habitats in terms of survival and growth often changes seasonally, or in relation to the developmental stage of the individual. Thus, selection should favour migration from freshwater to the sea when this reduces the value of μ/g, and habitat choices should be influenced by benefits and costs in each habitat. However, organisms only experience the situation where they currently are, and do not know the profitability of moving to distant feeding grounds unless this is innately determined through an epigenetic threshold type response or a genetically predetermined behaviour. Sea trout must therefore rely on additional cues, such as present growth or size, to bias their movements towards the appropriate feeding ground (Dodson, Aubin-Horth, Thériault, & Páez, 2013). Their response is fine-tuned through natural selection, although the response appears phenotypically plastic, allowing the fish to cope with environmental stochasticity and variation. However, the degree of plasticity is at least partly inherited and varies among populations (Fusco & Minelli, 2010). There is little knowledge on the extent of epigenetic effects on behavioural decisions (Baerwald et al., 2016), although Jonsson and Jonsson (2018) showed that the temperature experienced by Atlantic salmon embryos influences the timing of their homing migration years later, when they as adults return from the ocean to spawn in freshwater.

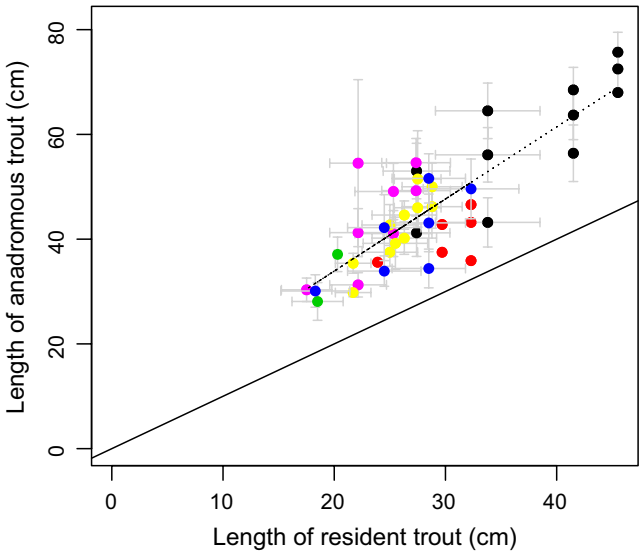


FIGURE 5 Correlation between mean length at age for resident and anadromous brown trout at the River Hals (green), River Vosso (yellow), River Burrishoole (red), River Tamar (pink), River Bresle (black) and River Oir (blue). The solid line represents the 1:1 line. The dotted line represents the relative growth gain attributable to sea migration, with a slope estimated at 1.377 (*SD*: 0.138) and significantly different from 1 (χ^2 = 318.2, *df* = 1, *p* = .006). Values are presented ± 1 *SD*, except for River Burrishoole. See Table S1 for details. Figure appears in colour in the online version only

3.2 | Migration to improve growth

Growth of trout depends largely on food consumption and temperature. Young trout experiencing reduced growth because of food restrictions may either move to a more profitable feeding habitat or attain sexual maturation at an early age to make the most of a poor environment (Jonsson, 1985). Thus, feeding migration is a viable alternative if distant habitats provide improved growth opportunities without a disproportional decrease in survival (Jonsson & Jonsson, 1993). Growth is typically higher at sea than in freshwater. For instance, length increase during the second year in freshwater is typically 6 cm in Southern Norway (L'Abee-Lund et al., 1989), which is approximately half the length increase obtained by immature trout spending their second year at sea (Jonsson & Jonsson, 2011; Poole et al., 1996), but growth decreases with age and sexual maturation. In northern Norway, the difference between freshwater and marine growth may be even larger (Berg & Jonsson, 1990). In addition to better feeding opportunities, growth at sea may be less constrained because of reduced population density and intraspecific competition in northern temperate and sub-Arctic areas. In some systems, lakes may also offer better growing condition than the nearby mainstream river and reduced costs of migration compared to seaward migration (e.g. short migration distance, low predation). A similar pattern may hold true for brown trout moving from tributaries to the mainstream, further downstream, in large river systems. Distinct populations of adfluvial trout have been identified, such as the Dollaghan trout in Lough Neagh, northern Ireland, and the Croneen trout in Lough Derg on the Shannon, Ireland (Ferguson, 2004). Such a trade-off may also be driving lacustrine migration in landlocked trout populations, as observed in Lake Geneva (Champigneulle, Buttiker, Durand, & Melhaoui, 1999).

The aggregation of six data sets from across Europe allowed us to highlight some new patterns (Figure 5). Within our six populations, we observe a general pattern that emerges in the form of a positive correlation in body length between anadromous and resident trout. This means that rivers with large resident trout also produce large anadromous trout. Moreover, the relative growth gained by the sea migration (i.e. the deviation from the 1:1 line in Figure 5) is larger in populations of large brown trout. Apparently, for anadromy to be a viable life-history tactic, the growth rate of anadromous fish must be higher than that of corresponding freshwater residents.

3.3 | Migration can improve survival

Mortality is higher during the marine migration than in freshwater, with sea trout facing high predation rates during early sea migration when they are small and cross the estuarine zone. For instance, precise estimates from Black Brows Beck, Lake District, England, showed that the instantaneous rate of survival of brown trout was about 0.88% day^{-1} during the second year in freshwater while the return rate of post-smolts at sea averages 0.25% day^{-1} (Elliott, 1993). Aldvén, Hedger, Økland, Rivinoja, and Höjesjö (2015) detected a significantly higher mortality rate in brown trout smolts moving from the river into a shallow estuary (mortality 26%–51%)

than in smolts entering a deep fjord (17.5%–29.2%). Dieperink, Bak, Pedersen, Pedersen, and Pedersen (2002), Dieperink, Pedersen, and Pedersen (2001) studied avian predation on emigrating wild and domesticated sea trout post-smolts in fjords of the western Baltic Sea and North Sea. In total, 65% of the post-smolts were eaten by fish-eating birds, and during the first 2 days after entering the sea, both wild and domesticated post-smolts suffered a daily predation rate estimated at 20%–34%. Thus, the trout appeared to experience a transient period with elevated risk of predation immediately after exposure to sea water. However, in other places, the early mortality is noticeably lower. Survival of smolts migrating through Randers and Mariager Fjord in Denmark showed survivals between 76% and 80% 30 days after fjord entry and in Poole Harbour in England 88% of the trout smolts entering the estuary made the 12 km transition to the open sea (Aarestrup, Baktoft, Koed, del Villar-Guerra, & Thorstad, 2014; Lauridsen et al., 2017; del Villar-Guerra, Aarestrup, Skov, & Koed, 2013). Predation rates appear to be influenced by the time and size at migration, and sea trout of the River Imsa, Norway, exhibit highest survival if migrating in May (ca. 15% until river return) and low survival if migrating to the sea between July and December (ca. 2%) (Jonsson & Jonsson, 2009a). However, in Gudsø Stream, Denmark, the return rates of spring and autumn migrants were similar (Birnie Gauvin & Aarestrup, 2018). This suggests difference in autumn mortality between rivers. Also, one would expect that sea migration in the autumn would benefit other fitness components, such as growth, and compensate for this potential high initial migration cost.

By migrating, sea trout can avoid adverse environmental conditions in the home stream, such as winter icing-up of streams or summer drought. For instance, in small streams regularly experiencing summer drought, sea trout can migrate to sea at a small size early in life and in this way avoid poor growth and survival conditions (Jonsson et al., 2001; Landergren, 2004; Titus & Mosegaard, 1992). This pattern resembles the strategy followed by some Pacific salmonids, such as pink salmon (*Oncorhynchus gorbuscha*, Salmonidae) and chum salmon (*Oncorhynchus keta*, Salmonidae), which both start their seaward migration early in life. Trout from streams with low water level during winter may migrate to a neighbouring watercourse for overwintering (Aldvén & Davidsen, 2017) or stay in marine waters (Eldøy et al., 2017; Jonsson et al., 2018; Olsen et al., 2006).

3.4 | Improved fecundity

Fecundity, or number of ova per unit length, changes between stocks (Fahy, 1985; Poole, Byrne, Dillane, Whelan, & Gargan, 2002) and between stocks in different regions (Jonsson & Jonsson, 1999; Solomon, 1997). But, with larger body size, sea trout increase their gamete production and direct competitive ability on the spawning ground, and thus obtain augmented reproductive success (Fleming, 1996; Gross, 1987; Hutchings & Myers, 1985). For instance, mean fecundity of sea trout from Vangsvatnet Lake, Norway, was 1,790 eggs compared to 330 eggs for nonanadromous females of similar age (i.e. <20%; Jonsson, 1981, 1985). Egg size increases with the size of the mother, and with increasing egg size, early growth and viability of offspring increase (Bagenal, 1969; Segers & Taborsky, 2011). However, these relationships are dependent on the female life history, with females investing in larger ova as the fish become larger and older. It seems that anadromous females had smaller ova compared with freshwater-resident females of similar body size (i.e. older fish) and achieved higher fecundity as they grew bigger (Acolas, Roussel, & Baglinière, 2008). Another advantage for the offspring of anadromous females may come from an earlier hatching date in the season, as reported in anadromous brown trout (Jonsson & Jonsson, 1999) and rainbow trout relative to sympatric resident trout (Zimmerman & Reeves, 2000). A longer spawning period in resident trout may buffer this phenological difference in some cases, for example River Oir, France (Maisse et al., 1991). Less is known about the production of male milt and spermatozoa in brown trout, although differences in sperm count were observed between stocks and the length of the spawning migration (Jonsson & Jonsson, 2006) and a negative trend was linked with size and age of males, possibly indicating a lower fertilizing ability of older fish within any one stock (Poole & Dillane, 1998).

3.5 | The energy surplus hypothesis

Several studies suggest that anadromy in brown trout is triggered by energy limitation in natal rivers (reviewed by Dodson et al. (2013)) and can be terminated if the relative advantage of migration changes (Sandlund & Jonsson, 2016). Some early studies documented an asymptotic size at one year, which is limited by the carrying capacity of the river (Baglinière & Maisse, 1990). Thus, to meet their energy requirements and grow further, individuals should change habitat and move towards a more productive habitat further downstream in the watershed or at sea (Baglinière & Maisse, 2002). Brown trout appear to favour a migration strategy when the energy surplus useable for growth becomes low (Forseth, Nesje, Jonsson, & Hårsaker, 1999; Jonsson & Jonsson, 1993).

Experimentally, Davidsen et al. (2014) induced migration by decreasing ration size during the 6 months prior to smolting. Similarly, Jones, Bergman, and Greenberg (2015) demonstrated that reduced winter and spring feeding increased the tendency to smoltify for lake feeding brown trout from the River Klarälven, Sweden. In contrast, another experiment reported that trout facing food restriction in late autumn exhibited lower rate of silvering, which is indicative of a delay in smolting (Näslund, Sundström, & Johnsson, 2015). Thus, winter/beginning of spring appears to be a critical period when the decision is made about whether to smolt and migrate to a better feeding area. These experimental findings contrast with Thorpe and Metcalfe's (1998) hypothesis that autumn is the critical time in Atlantic salmon, when decisions of migration versus maturation are taken. This implies that brown trout are more plastic and energy intake during winter and spring may over-rule an initial decision, depending on the energetic state of the fish (cf. Jonsson, Jonsson, & Finstad, 2013). In contrast, rearing brown trout in aquaculture with optimum rations reduces the probability of smolting,

leads to early maturation and lowers the return rates from sea releases (Byrne, Poole, Dillane, & Whelan, 2002; Mills, Piggins, & Cross, 1990).

Within brown trout populations, fast growers tend to migrate at a younger age, and typically smaller size than slow growers (Jonsson, 1985; Økland, Jonsson, Jensen, & Hansen, 1993), and within a given cohort, larger juveniles tend to undertake longer migrations (Ombredane et al., 1996). Individuals with a high metabolic rate may migrate downstream earlier as their energy demands more rapidly exceed those available in their current habitat than in smaller trout (Ferguson, Reed, McGinnity, & Prodöhl, 2017; Forseth et al., 1999; Peiman et al., 2017). Sea trout smolts have very low energy density at the time of migration (ca. 350 kJ/100 g wet mass), which is similar to that of resident trout after spawning (Jonsson & Jonsson, 1997, 1998). This is due to a low lipid density (ca. 1.5 g/100 g wet mass), which may contribute to the compensatory growth exhibited by sea trout during the first weeks at sea (Marco-Rius, Caballero, Moran, & Leaniz, 2012). In brook trout (*Salvelinus fontinalis*, Salmonidae), Morinville and Rasmussen (2003) reported that in the year before migration, migrant brook trout have consumption rates 1.4 times higher than those of resident brook trout. However, migrants have lower growth efficiencies (ratio of growth to consumption) than residents, indicating that migrants have higher metabolic costs, and relatively less surplus energy available at the time the migrations commences.

Individual growth rate better integrates the mechanisms underlying migration decision whereas body size is more strongly related to survival in trout (Acolas, Labonne, Baglinière, & Roussel, 2012). Intrinsic differences between individuals explain why migrants and residents differ in body size in many partial migratory species

TABLE 1 Sex ratio of smolts and sexually mature sea trout as reported from various rivers across Europe

River	Life stage	Per cent females	Reference
Voss, Norway	Smolts	58	Jonsson (1985)
Tweed, Scotland	Smolts	59	Campbell (1977)
Nybroån, Sweden	Smolts	61	Dellefors (1996)
Istra, Norway	Smolts	61	Jensen (1968)
Bresle, France	Smolts	62	Quéméré et al. (2011)
Jutland (several streams), Denmark	Smolts	75	Nielsen (1994)
Verkeån, Sweden	Smolts	75	Svärdson (1966)
Vindelälven, Sweden	Smolts	73	D. Palm (personal communication)
Mean ± 1 *SD*	Smolts	65.5 ± 7.4	
Mørfjær, Sweden	Adult	44	Jonsson et al. (2018)
Själsöån, Sweden	Adult	48	Rubin et al. (2005)
Urvold lake, Norway	Adult	52	J. G. Davidsen (personal communication)
Bresle, France	Adult	55	Quéméré et al. (2011)
Bottenvassdraget, Norway	Adult	56	J. G. Davidsen (personal communication)
Saltdalselva, Norway	Adult	58	J. G. Davidsen (personal communication)
Vindelälven, Sweden	Adult	61	Norrfors fishladder, Vattenfall Vattenkraft AB
Åvaån, Sweden	Adult	63	Alm (1950)
Ihra, Sweden	Adult	64	Hessle (1935)
Voss, Norway	Adult	66	Jonsson (1985)
Verkeån, Sweden	Adult	73	Svärdson (1966)
Vistula, Poland	Adult	76	Svärdson (1966)
Oir, France	Adult	79	F. Marchand (personal communication)
Mean ± 1 *SD*	Adult	61.2 ± 10.6	

(Chapman et al., 2012). Improved feeding opportunities and growth is thus the main benefit of anadromy for fish spawning in freshwater (Frier, 1994; Gross, Coleman, & McDowall, 1988).

Size may also interact with the ability of juveniles to establish and hold territories; thus, smaller and/or younger parr may be forced to leave the stream by larger and/or older conspecifics (Landergren, 2004). In Atlantic salmon, some populations exhibit a bimodality in size by the end of the first growing season (Baglinière & Maisse, 1985). Individuals from the upper mode, that is large juveniles, smolt and migrate to sea the following spring (Baglinière & Maisse, 1985; Thorpe, Talbot, & Villarreal, 1982). Atlantic salmon appear to smolt when the young have reached a critical size, although this pattern may not be detected in slower growing populations of northern Europe (Økland et al., 1993). This is probably because survival at sea is strongly size dependent (Flaten et al., 2016; Jonsson et al., 2016). In trout, it is unknown to what degree size influences age at smolting (Figure 4). Juvenile size bimodality has not been detected at the end of the growth season (Baglinière, Prévost, & Maisse, 1994). This suggests that the migration decision may be taken later in trout, highlighting the greater flexibility of trout life history compared to Atlantic salmon (Baglinière et al., 2001).

4 | SEX-SPECIFIC RESPONSE

Skewed sex ratios are commonly observed within the anadromous and resident components of partially migratory brown trout populations. The skewed sex ratios result from differences in physiological constraints and life-history trajectories in males and females. The fitness of females appears more closely associated with body size than in males. Although the same environmental conditions interact with threshold limits to determine individual life histories, the mechanisms selecting for migration or residency differ between the sexes. This results in sexually divergent thresholds and rates of anadromy (Jonsson et al., 2001).

4.1 | Bias in sex ratio

Although the sex ratio of parr is even in brown trout, there appears to be a female surplus among emigrating smolts (Cucherousset et al., 2005; Jonsson, 1985; Klemetsen et al., 2003). In northern France, the percentage of females among migrating smolts varies between 57% and 67% (Euzenat, Fournel, & Richard, 1999; Quéméré, Gentil, & Launey, 2011), which fits well with what is found elsewhere (Table 1). Also, females typically outnumber males among adults entering streams for spawning (Campbell, 1977; Euzenat, Fournel, & Fagard, 2006; Jensen, 1968; Jonsson, 1985; Mills et al., 1990; Okumuş, Kurtoglu, & Atasaral, 2006; Poole et al., 2007). On the spawning grounds, however, the operational sex ratio may be skewed in favour of males because they stay longer and if possible, spawn with several females (Aarestrup & Jepsen, 1998).

The size of the stream used for spawning may influence spawning success and therefore indirectly the sex ratio, with male surplus reported in several small streams (Jonsson et al., 2018; Rubin, Glimsäter, & Jarvi, 2005). The highest proportion of females among the anadromous trout are found in the nutrient rich and productive streams and large rivers of the Baltic and the North Sea areas (Table 1), and this bias may be larger when the high proportion of repeat spawners, as postspawning survival is greater in females than in males. In small streams, males mature younger and smaller than females, and relatively more males will therefore survive to adulthood (Jonsson, 1985; Jonsson & Jonsson, 2015). Where there is a female surplus among the smolts, it may be evened out among anadromous adults because males mature younger than females and more will therefore survive to adulthood (Jonsson et al., 2018).

Anadromous females typically outnumber anadromous males in larger streams, and the same is reported from other species of partly migratory trout and charr, such as rainbow trout (McMillan, Katz, & Pess, 2007; Rundio, Williams, Pearse, & Lindley, 2012; Van Doornik, Berejikian, & Campbell, 2013), Arctic charr (Nordeng, 1983), whitespotted charr (*Salvelinus leucomaenis*, Salmonidae; Tamate & Maekawa, 2004) and some Atlantic salmon populations (Jonsson, Jonsson, & Hansen, 1998), although exceptions occurs (J.-L. Bagliniere, personal communication). Dodson et al. (2013) noted an increase in male anadromy of brook trout towards the north. This has not yet been investigated for brown trout.

4.2 | Strong size dependence in females

Large female size is selected by natural selection as reproductive success is more strongly associated with body size in females than males (Jonsson, 1985; Kendall et al., 2014). Furthermore, body size variation is smaller in females than in males. This may be because females do not exhibit alternative spawning tactics (sneaking versus fighting) as males do (McLean, Bentzen, & Quinn, 2004). Furthermore, the gonad development of females requires more energy (Baglinière et al., 2001; Fleming, 1996; Prouzet, LeBail, & Heydorff, 1984). Thus, females are more likely to migrate to more food rich areas and stay there for longer periods of time to grow larger before spawning (Bordeleau et al., 2018; Cucherousset et al., 2005; Ferguson, 2006; Northcote, 1992). Undertaking a longer and more risky sea migration may reduce survival, resulting in relatively few anadromous female trout returning as adults. Higher marine mortality in females than males has been reported for anadromous whitespotted charr by Tamate and Maekawa (2004), but no empirical evidence is available for sea trout. On the other hand, postspawning survival is higher in female charr (and salmon) than in males, which may also hold for brown trout. Thus, sex ratio of repeat spawners may be even more skewed in favour of females (Euzenat et al., 1999).

4.3 | An alternative strategy in males

A large male size may be favoured because of both natural and sexual selection (Young, 2005). They are favoured by natural selection

because large males have larger testes (Jonsson & Jonsson, 2005, 1997), win spawning contests more often and therefore spawn more times than smaller males (Fleming, 1996). They are favoured by sexual selection because females prefer large males as partners (Petersson, Järvi, Olsén, Mayer, & Hedenskog, 1999; Serbezov, Bernatchez, Olsen, & Vøllestad, 2010) and large males gain better access to females due to higher fighting success. On the other hand, male size is not directly associated with reproductive success (Poole & Dillane, 1998) even though large males do enjoy strong competitive advantages over smaller resident males when fighting for mates (Bohlin, Dellefors, & Faremo, 1990). Some males may adopt an alternative spawning behaviour (Dominey, 1984; Gross, 1991). While large males gain access to females through fighting, small resident males effectively employ a sneaking tactic to the same ends (Olsén, Järvi, Mayer, Petersson, & Kroon, 1998), avoiding the risks of migration, and breeding at a younger age (Foote, Brown, & Wood, 1997). However, "precocious" maturation is less pronounced in brown trout than in Atlantic salmon, where males can mature before the age of 1 (Baglinière & Maisse, 1985). Since maturation and smolting may be considered competing developments in terms of energy allocation and physiology, the energy requirements for smolting after maturing may be too large to allow migration within a reasonable seasonal schedule. Indeed, maturation in brown trout correlates with delayed or reduced rates of smolting (Bohlin et al., 1990; Cucherousset et al., 2005; Dellefors & Faremo, 1988; Jonsson, 1985), but nevertheless does happen.

Intermediate-sized individuals, in contrast to large or small individuals, may be ineffective at both fighting and sneaking mating strategies, putting them at a competitive disadvantage and maintaining the separation of two distinct male phenotypes as observed within many wild salmonid populations (Gross, 1985). It is possible that where intermediate-sized mature males are present on spawning grounds, they utilize female mimicry in order to approach females without attracting the aggression of large dominant males (Esteve, 2005). This behaviour, which is associated with altered male colouration resembling that of mature females, has been reported in Arctic charr, pink salmon, chum salmon and red-spotted masu salmon (*Oncorhynchus masou ishikawae*, Salmonidae; Kano, Shimizu, & Kondou, 2006; Keenleyside & Dupuis, 1988; Sigurjónsdóttir & Gunnarsson, 1989).

5 | ENVIRONMENTAL DRIVERS OF ANADROMY IN JUVENILES

Anadromy and residency in brown trout are considered alternative tactics within a single strategy (Dodson et al., 2013). The decision to migrate to sea results from a trade-off between mortality and growth in fresh and salt waters so that the overall fitness is maximized, and individuals must use proximate cues to adopt the most appropriate life history (Kendall et al., 2014). Environmental factors influencing growth in early life are probably the main cues on which the decision is made (Baglinière et al., 2001; Ferguson et al., 2017; Jonsson & Jonsson, 1993).

5.1 | Food availability

Both empirical and experimental studies have reported negative correlations between the proportion of migratory trout and food availability in the natal freshwater system (review in Ferguson et al. (2017)). For instance, the migration of brown trout between a tributary where they spawned and the main river ceased when the growth opportunities in the main river decreased because of damming and reduced flow in the main river (Jonsson & Sandlund, 1979; Sandlund & Jonsson, 2016). Kendall et al. (2014) noted that food quality, which is energy value, may be as important as food quantity. Hence, resident trout appear to be abundant in the most productive areas, with a high invertebrate biomass. Where lakes are present, a lacustrine-adfluvial migration pattern often predominates (Ferguson, 2004; Ferguson et al., 2017; Gresswell, Liss, & Larson, 1994), as some lakes may offer good growth condition with a lower predation cost than sea migration. This is supported by the observation that stocking well fed, juvenile hatchery trout often produces freshwater-resident fish, but starving the fish before release induces a migratory behaviour (Davidsen et al., 2014; Larsson, Serrano, & Eriksson, 2011). Thus, growth opportunities in the local habitat play an important role in the decision whether to migrate or not (Larsson et al., 2011). Also, environmental stochasticity in the river, such as winter frost or summer drought, can seasonally constrain feeding opportunities and initiate migration. In this case, trout may opt for migration to the marine environment, which may appear more stable and protective against harsh physical conditions (Aldvén & Davidsen, 2017; Ferguson et al., 2017).

5.2 | Thermal condition

Temperature is a key factor structuring freshwater ecosystems. It may influence migratory decisions, with both absolute temperature and variation in temperature being important (Kendall et al., 2014; Morita, Tamate, Kuroki, & Nagasawa, 2014). Optimum temperature for growth of juvenile 1 g brown trout is found to be 13–14°C (Forseth et al., 2009), but it can be high if energy consumption is very high such as in piscivorous trout (Forseth & Jonsson, 1994), and lower if the fish are particularly large or feeding is reduced (Morita, Fukuwaka, Tanimata, & Yamamura, 2010). Temperature is clearly linked to food availability, feeding activity, metabolism and lipid storage (Ferguson et al., 2017). High temperature allows higher food consumption but also increases maintenance costs and may accelerate energy shortages. Furthermore, standard metabolic rate may be affected by the temperature experienced by the yolk feeding larvae (Álvarez, Cano, & Nicieza, 2006). Thus, unless food production increases by the same order of magnitude, individuals may not be able to meet their energetic requirements when temperature increases. However, this pattern may be attenuated by temperature itself, as abnormal temperature may also act as a physiological stressor and induce migration (Peiman et al., 2017). However, an increase in temperature may fuel the production of invertebrates and thereby offer improved feeding opportunities for resident trout, as

explained above (Morita et al., 2014; Olsson, Greenberg, Bergman, & Wysujack, 2006). But further projected increases in river water temperature above the optimal temperature for growth will likely decrease growth, body length and increase age at smolting, and ultimately reduce the survival of trout (Davidson, Hazlewood, & Cove, 2007; Fealy et al., 2010). However, the relative contribution of temperature to trout growth compared to other environmental drivers remains difficult to quantify. In Atlantic salmon, Bal, Rivot, Prévost, Piou, and Baglinière (2011) reported that variation in freshwater temperature had only a small effect on the growth of juveniles compared to variation in salmonid density.

5.3 | Flow condition

In the rivers, trout are largely ambush predators, relying on the flow to bring food to them although they are more active hunters than Atlantic salmon. In darkness, they can pick zoobenthos on the bottom. The nursery habitat may differ between resident and anadromous conspecifics as reported by Morinville and Rasmussen (2003). They studied brook trout and found that the young of migratory trout used faster running water than young resident trout, and that they also fed on different food items. This pattern is expected to come from intrinsic differences in metabolic requirement and is not indicative of an effect of flow condition on migration decision. High flow often correlates with high availability in food resource, which influences the opportunities for growth (Kendall et al., 2014; Morinville & Rasmussen, 2003). Furthermore, flow may have an effect on anadromy in rainbow trout, at least in climate zones where summer flows are a limiting factor (Kendall et al., 2014). Flow that regularly reaches zero may represent a population bottleneck for nonmigratory fishes (Courter, Justice, & Cramer, 2009), and low flow may explain the small size at first smolting of brown trout in some small streams (Borgstrøm & Heggenes, 1988; Jonsson et al., 2001). More generally, unsuitable flow condition in streams is likely to drive the propensity to migrate to sea, for example due to low flow, or highly variable flow conditions in the home stream, or a reduction in suitable habitat and high keen competition from conspecifics (density dependence effect).

So far, there are empirical evidences of a positive correlation between flow and the number of migrating smolts in brown trout. In the Danish River Lilleaa, the migration speed of wild sea trout smolts was positively correlated with water discharge (Aarestrup, Nielsen, & Koed, 2002). But when the flow remains low, trout may wait until the temperature increases over a certain level (Aarestrup et al., 2002). In a Swedish west coast stream, smolts remained in the rivers during years with low precipitation until the temperature reached 10°C, and migration increased thereafter irrespective of the discharge (Aldvén et al., 2015). A shift from nocturnal to diurnal migration appears to occur when the water temperature is 12–13°C and is most pronounced in large smolts (Haraldstad, Kroglund, Kristensen, Jonsson, & Haugen, 2017). Single large temperature increases can also initiate a daytime migration (Aarestrup et al., 2002). Water temperature and flow influence the phenology of the sea trout smolt migrations. Temperature regulates the timing of the start and the end of the migration period while water level, change in water flow and water temperature influence the number of smolts migrating each day (Byrne et al., 2004; Jonsson & Jonsson, 2002).

5.4 | Density dependence

The food availability interacts with fish density in limiting the resources available per capita. Higher competition for food and space at high density results in fewer residents, with migrants maximizing growth by moving into the sea (Ferguson et al., 2017; Olsson et al., 2006). During periods of drought or hydropower regulation, density will increase. Stradmeyer, Höjesjö, Griffiths, Gilvear, and Armstrong (2008) showed how the importance of dominance status for maintaining food intake increases as the polarization between the top ranked fish and others increased. As a result, fewer fish will mature and become residents; thus, migration may be an alternative (Jonsson & Jonsson, 1993).

5.5 | Interspecific competition

Similarly, competing species may also influence the proportion of brown trout that migrate, mediated through a density dependence process (Olsson et al., 2006). Young brown trout and Atlantic salmon compete for food and space in rivers, as evidenced by the spatial segregation observed between the two species (Jonsson & Jonsson, 2011). Young Atlantic salmon are mainly found in shallow, fast-flowing habitats of the main river while young trout colonize tributaries and headwaters (Baglinière & Arribe-Moutounet, 1985; Baglinière & Champigneulle, 1982; Kalleberg, 1958). In the Shelligan Burn (Scotland), the density of young Atlantic salmon was negatively correlated with that of young trout (Egglishaw & Shackley, 1982). Brown trout are territorial and very aggressive, and through interference, they constrain young Atlantic salmon from shallow, slow-flowing areas (Harwood, Metcalfe, Armstrong, & Griffiths, 2001; Heggenes, Baglinière, & Cunjak, 1999; Houde, Wilson, & Neff, 2017; Kalleberg, 1958). This trend is accentuated by the early hatching of trout (Baglinière et al., 1994), which are larger and have already established a territory by the time Atlantic salmon fry emerge. Furthermore, when brown trout are removed, young Atlantic salmon expand their habitat into former trout-defended areas, that is competitive release (Hearn, 1987; Kennedy & Strange, 1986). Experimentally, Gibson and Erkinaro (2009) showed that brown trout were four times more aggressive than corresponding Atlantic salmon. As a result of their more aggressive behaviour and larger size, brown trout have a competitive advantage in slow flowing, shallow areas along stream banks and pools where they monopolize the food resources (Gibson & Erkinaro, 2009; Höjesjö, Stradmeyer, Griffiths, & Armstrong, 2010). Atlantic salmon, on the other hand, make more use of cover, deep pools and fast-flowing riffles where food is difficult to defend. In addition, their more streamlined body shape and larger pectoral fins are assumed to give young Atlantic salmon a selective advantage in rapidly flowing rivers (Karlström, 1977), and they may outcompete

trout in fast-flowing streams (Montorio, Evanno, & Nevoux, 2018). The interaction between young brown trout and Atlantic salmon in rivers is adversely competitive; that is, increased abundance of the one leads to a decrease in abundance of the other. This is exemplified in formerly acidified rivers treated with calcium carbonate (limestone powder). As the abundance of Atlantic salmon increased with time, the density of brown trout decreased (Hesthagen, Larsen, Bolstad, Fiske, & Jonsson, 2017). However, when the abundance of Atlantic salmon increases at the expense of brown trout, the total output of salmonid smolts increases (cf. Kennedy & Strange, 1986).

The aggressiveness of brown trout is energetically costly. Their high-energy use is assumed to be the main reason why brown trout are outcompeted by Arctic charr because of a much lower growth efficiency in cold, food limited habitats (Finstad et al., 2011). In shallow, temperate localities richer in food, on the other hand, brown trout outcompete Arctic charr because of its higher aggressiveness. In sympatry, the two segregate spatially, with charrs shifting to the pelagic or the profundal zone (Heggberget, 1984; Klemetsen et al., 2003; Langeland, L'Abée-Lund, Jonsson, & Jonsson, 1991).

There is also competition between grayling (*Thymallus thymallus*, Salmonidae) and brown trout. Mäki-Petäys, Vehanen, and Muotka (2000) suggested that competition between these species increases in streams during winter when ice decreases the habitat availability. Competition between the two species may be a reason for their partial segregation in rivers (Greenberg, Svendsen, & Harby, 1996). However, recruitment of grayling and trout was positively associated in an English chalk stream (Bašić, Britton, Cove, Ibbotson, & Gregory, 2018). Also, Alpine bullhead (*Cottus poecilopus*, Cottidae) is a strong competitor to juvenile brown trout where these species co-occur (Hesthagen & Heggenes, 2003; Holmen, Olsen, & Vøllestad, 2003). For instance, Holmen et al. (2003) reported that brown trout density was five to 10 times higher at the upper, allopatric site than in downstream areas where it lived in sympatry with the Alpine bullhead. Diet composition suggested that brown trout in sympatry with Alpine bullhead foraged more on invertebrate drift and surface arthropods than allopatric brown trout did.

In addition, novel species that invade brown trout areas, naturally or because of human-mediated releases, may influence brown trout migration and habitat use. Brown trout living in sympatry with brook trout consumed more terrestrial prey, and had smaller home ranges and a stouter body shape (Závorka et al., 2017). Sympatric brown trout also had lower specific growth rates, suggesting a lower fitness. Other introduced species, such as rainbow trout affect brown trout negatively. Blanchet, Loot, Grenouillet, and Brosse (2007) found by use of laboratory and field studies that rainbow trout significantly affected native brown trout habitat selection and apparent survival. In contrast, Baran, Delacoste, Lascaux, Bauba, and Segura (1995) demonstrated a competition advantage of the brown trout in mountainous rivers when the two species live in sympatry. The more similar the ecology of the interacting species, the greater the impact of competition is.

There are examples of rivers where Atlantic salmon and resident trout co-exist, but little or no sea trout run is observed, as in Ireland and Brittany (France). In the Irish systems, the presence of lakes and running river sections may promote habitat segregation and reduce interspecific competition while in large salmon rivers, the occurrence of sea trout is often restricted to the lower stretches and to small tributaries close to or directly entering an estuary (Fahy, 1985; Whelan, 1989). Similarly, the tree-like shape of the watersheds in Brittany, characterized by many small tributaries, may maximize segregation and reduce competition between the two species (Baglinière et al., 1994).

It is still unclear whether interspecific competition in freshwater influences the tendency to migrate to the sea. However, one may hypothesize that brown trout will exhibit a stronger tendency to migrate if their resource use in freshwater is constrained by competing species, as shown for increased competition from conspecifics (Olsson et al., 2006). Montorio et al. (2018) provided empirical evidence for interspecific competition–exclusion relationship. They found a negative effect of trout density on growth and survival in juveniles, but a positive effect of Atlantic salmon density on the probability of migration in young trout. They reported that in years following a high recruitment in salmon, the propensity of trout leaving the stream was high. Atlantic salmon may be a main competitor in temperate areas and Arctic charr in sub-Arctic and Arctic areas.

5.6 | Predation

The role of predators in shaping patterns of partial migration has been historically neglected (Chapman et al., 2012). However, if the decision to migrate is a balance between growth opportunities and mortality risk, increased predation in freshwater should select for anadromy in trout. Predation risk may constrain habitat use and thereby reduce individual growth (Johnsson, Rydeborg, & Sundström, 2004). Alternatively, high predation in freshwater may offer more resource per capita to the remaining individuals with an opposite effect on the opportunity for growth.

Predation is expected to be particularly high during the smolt run and in the first few days after the smolts reach sea water (Dieperink et al., 2002; Thorstad et al., 2016). If there are alternative prey, such as Atlantic salmon smolts migrating to sea at the same time, this may reduce the mortality and increase the fitness of sea trout (Jonsson & Jonsson, 2009b), or it may stimulate the aggregation of predators (Jepsen, Holthe, & Økland, 2006). Thus, although effects of predation on the life-history strategy of trout are not well studied, this does not mean that predation is unimportant in this respect.

6 | INFLUENCE OF THE MARINE ENVIRONMENT ON MIGRATION OUTCOME

The decision to migrate is a trade-off between benefit and cost. Costs associated with sea migrations include energy used for swimming and increased probability of death, for example owing to predation, parasitism and diseases, but also the physiological adjustments

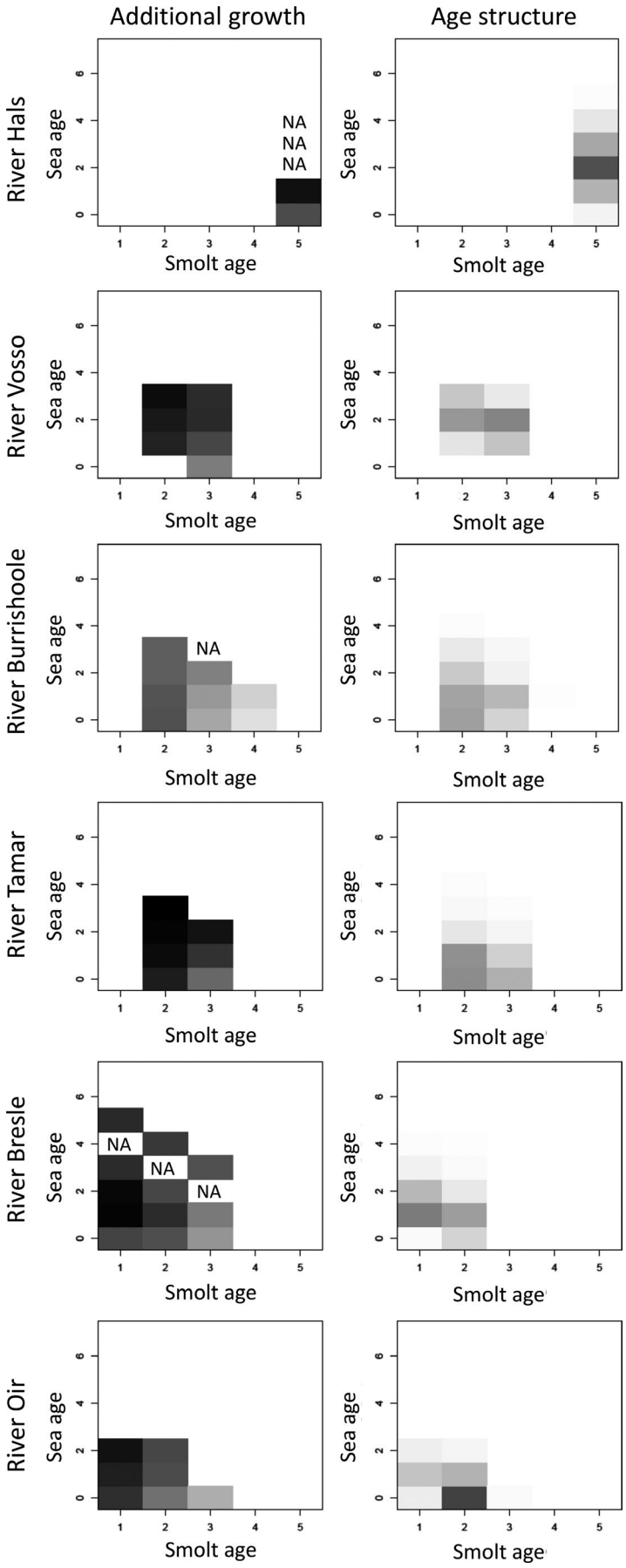


FIGURE 6 Characterization of the migration strategy in brown trout along a latitudinal gradient of populations: River Hals 70°N (Norway), River Vosso 60°N (Norway), River Burrishoole 54°N (Ireland), River Tamar 51°N (England), River Bresle 50°N (France) and River Oir 48°N (France). Left panel: relative additional growth for anadromous trout related to sea age and smolt age, expressed as a growth difference with resident trout of similar age. Some values are missing when no resident trout of a similar total age were caught. Right panel: age structure of returning anadromous trout, in terms of sea age and smolt age. The darker the cell, the higher the value

for salt excretion (Gross et al., 1988). Distance to the coast and deep sea areas may limit the distribution of sea trout. It is generally assumed that most anadromous brown trout feed in shallow waters within 100 km from the river mouth (Jonsson & Jonsson, 2011; Thorstad et al., 2016). Nevertheless, there are some evidences of large within- and between-population variations in marine migration distance (Jonsson & Jonsson, 2014; Kristensen et al., 2018; Potter, Campbell, Sumner, & Marshall, 2017; Prodöhl et al., 2017).

6.1 | Growth potential

Growth levels off with age and spawning history, but the difference in size between resident and anadromous trout increases with age (Figure 6, left panel). This suggests that the best growth strategy in brown trout would be to leave early and stay longer at sea. In the Burrishoole River (Ireland) and the River Bresle (France), fish with the combination of smolt age and sea age that results in the highest growth gain are well represented among the returning anadromous trout (Figure 6, right panel). However, some of these strategies are represented by a low proportion of trout. Data support a mismatch between the age-specific additional growth and the age structure of the anadromous trout in River Vosso (Norway), River Tamar (England) and River Oir (France). In these populations, data show a shorter marine sojourn and/or an older age at smolting than expected under the hypothesis of growth maximization. We argue that strong constraints in the marine environment, in terms of mortality, may select against growth maximization strategies. For instance, young smolts may be too small to escape length-biased predation, thus favouring late runners. Furthermore, marine survival may be too low to support long marine sojourns; that is, very few two sea winter sea trout may survive until spawning.

By driving the level of mortality and growth in trout that initiate seaward migration, the marine environment influences the balance between the cost and benefit of the time at sea. If the costs of feeding at sea exceed the gains, selection should favour freshwater residency (Gross et al., 1988). In only a few generations, altered environmental conditions can terminate the tendency to migrate (Olsson et al., 2006; Sandlund & Jonsson, 2016). The marine environment acts as a selective filter on anadromy, and any increase in mortality at sea is likely to contribute to the reduction in sea trout abundance over space and time.

6.2 | Seascape

Quéméré et al. (2016) explored effect of seascape, for example the marine landscape, on the connectivity of brown trout populations between rivers, and how the seascape influences the life history of brown trout across northern France. They found two genetically distinct populations that strongly differed in terms of migratory propensity and stock characteristics. Western populations mainly produce freshwater-resident trout and small sea trout (finnock, i.e. post-smolt returning in the same year as they went to sea for the first time), while eastern populations produce large sea trout that perform long sea sojourns. They hypothesized that such a pattern may be driven by the spatial arrangement and feeding opportunities of marine habitats, which promotes a clinal variation in migratory behaviour. In the highly productive Eastern basin of the English Channel, anadromous trout can achieve very large size and long sea sojourn, which may favour dispersal and gene flow among neighbouring streams. In the Western basin, marine feeding opportunities are poor and trout have evolved mainly a freshwater-resident life history (Quéméré et al., 2016). The dispersal barrier may act as a forcing factor for a distinct life history (Richardson, Urban, Bolnick, & Skelly, 2014). On the other hand, the rivers appear different, and habitat characteristics may also add to the variation observed. Fahy (1985) also observed differences in trout size, growth and condition between trout returning from different regions, such as the Irish Sea compared to the Irish west coast and even from different bays along the west coast (R. Poole, unpublished).

6.3 | Sea lice

The sea lice (*Lepeophtheirus salmonis*, Caligidae and *Caligus elongatus*, Caligidae) are natural parasites of sea trout that can propose major threats to trout in the marine environment. During the last 30 years, salmon farming has increased the abundance of sea lice (Finstad & Bjørn, 2011; Fjørtoft et al., 2017; Thorstad & Finstad, 2018; Thorstad et al., 2015; Tully, Poole, & Whelan, 1993; Tully, Poole, Whelan, & Merigoux, 1993). Sea lice induce ionoregulatory dysfunction, physiological stress, anaemia, reduced feeding and growth, changes in post-smolt behaviour, increased susceptibility to secondary infections, reduced disease resistance and ultimately mortality of individual sea trout (Finstad & Bjørn, 2011; ICES, 1997; Poole, Nolan, & Tully, 2000). Wild adult sea trout in farm-free areas exhibit relatively low sea lice levels (Gargan, Tully, & Poole, 2003; Schram, Knutsen, Heuch, & Mo, 1998). On the other hand, in farm-intensive areas, sea lice levels on wild sea trout are typically higher (Gargan et al., 2003; Moore et al., 2018; Tully et al., 1993; Tully & Whelan, 1993). Sea lice infestations in these areas regularly exceed more than 0.35 lice per gram of fish mass, initiating physiological disturbance to the trout with weight range from 16 to 70 g (Wells et al., 2006, 2007). At higher lice levels, mortality may occur (Taranger et al., 2015). The sea lice levels on wild sea trout are particularly high within 30 km of salmon farms, but elevated lice infestations extend beyond this distance (Gargan et al., 2003; Moore et al., 2018; Serra-Llinares, Bjørn, Finstad, Nilsen, & Asplin, 2016; Serra-Llinares et al., 2014; Tully, Gargan, Poole, & Whelan, 1999). Therefore, sea lice in intensively farmed areas negatively impact wild sea trout through a suite of primary and secondary impacts reducing marine growth and survival of sea-run fish (Halttunen et al., 2018; Shephard, MacIntyre, & Gargan, 2016). Quantification of these impacts remains a challenge, although population-level effects have been quantified in Atlantic salmon using field experiments (Krkošek et al., 2013; Skilbrei et al., 2013; Vollset et al., 2016), showing higher survival in groups of antiparasitically treated fish relative to nontreated

control groups. Reduced growth and increased mortality in the marine environment decrease the benefits of marine migration for sea trout (Halttunen et al., 2018), and high sea lice levels might select against anadromy. In some populations, immature anadromous trout return frequently to rivers during the growth season. Such "premature returning" may be an early warning signal of heavy salmon lice infestations (Halttunen et al., 2018; Maisse et al., 1991). Sea lice-induced effects on sea trout may in extreme cases lead to local loss of anadromous trout and a transition to entirely resident trout populations (discussed in Poole et al. (2007) with reference to the Burrishoole sea trout stock). However, recent studies showed the complexity of the relationship between brown trout and sea lice infestations in the wild (relationship between size of trout and distance of farm cage) and emphasized the requirement of further research to quantify these effects (Moore et al., 2018).

7 | INFLUENCE OF THE SPAWNING HABITAT ON REPRODUCTION OUTCOME

Marine migration is a strategy that allows brown trout to escape from, or reduce the influence of, density dependence and resource limitation in freshwater, and by that maximize reproductive output (Jonsson & Jonsson, 2006; Lobón-Cerviá, 2007; Marco-Rius, Caballero, Moran, & Leaniz, 2013). But to reproduce, trout must return to freshwater and compete for access to suitable spawning sites and mates. Intense spawning competition may introduce both density- and frequency-dependant pressures (Berejikian et al., 2010; Foote et al., 1997; Gross, 1985), where body size is important for determining reproductive success (Serbezov, Jorde, Bernatchez, Olsen, & Vøllestad, 2012). Interference competition generally favours large individuals (Olsén et al., 1998); however, in small shallow tributaries, small resident trout may have higher fitness because these habitats are less accessible for large individuals. In populations dominated by individuals with short sea sojourns, there is larger spatial overlap between the spawning grounds of resident and anadromous trout than in populations dominated by longer sea sojourn. Interbreeding between the two phenotypes (Charles, Roussel, Lebel, Baglinière, & Ombredane, 2006) produces fertile offspring (Ombredane et al., 1996), but these offspring have reduced migration probability because the migratory strategy is partly inherited (Baglinière et al., 2001; Jonsson, 1982). Size-specific spawning success of both sexes is influenced by habitat characteristics as well as the competitive ability and density of the competitors, although contrasting selective mechanisms operate on males and females (Jonsson & Jonsson, 2015). Hence, the effect of each of these selective variables is sex-specific and determined by both the environment and the population structure (Young, 2005). Thus, spawning requirements play an important role in determining the frequency, abundance and sex ratio of anadromous brown trout (Jonsson & Jonsson, 2015).

7.1 | Habitat suitability

In order to breed successfully, female brown trout require a specific combination of hydrological conditions and substrate composition (Baglinière, Champigneulle, & Nihouarn, 1979; Gauthey et al., 2015; Montgomery, Buffington, Peterson, Schuett-Hames, & Quinn, 1996; Tappel & Bjornn, 1983). In many circumstances, the availability of habitat that adequately meets these conditions represents the primary factor limiting the size of salmonid populations (Buffington, Montgomery, & Greenberg, 2004; Kondolf & Wolman, 1993).

Despite their difference in body size, the specific spawning habitat requirements of anadromous trout versus freshwater-resident trout have hardly been studied (Nika, Virbickas, & Kontautas, 2011; Walker & Bayliss, 2007). It seems clear, however, that growth associated with anadromy will represent differing reproductive advantages depending on the nature of available spawning habitat.

The extra energy expenditure of migrating a longer distance is indicated by the gradual decrease in the condition factor of anadromous brown trout with increasing migratory distance inland. The gonadosomatic index of males (I = mass of gonads/somatic mass) decreases with migratory distance (Jonsson & Jonsson, 2006). Bohlin, Pettersson, and Degerman (2001) hypothesized that the fitness of migrants is negatively related to the altitude of the spawning area because of migratory costs, and in support of this, they found that anadromous trout were replaced by nonanadromous conspecifics at an altitude of ca. 150 m in southern Sweden. More than distance itself, it is the energetic demand required to reach the spawning ground that matters. As such, the cumulative effect of barriers (natural or artificial) can greatly impede sea trout migration inland in fragmented rivers.

7.2 | Flow condition and scouring risk

Prior to spawning, female salmonids flex their flanks and tail fin to excavate depressions (nests) in the streambed into which eggs are deposited. Due to the allometric relationship between fish length and caudal thrust, salmonid females can construct their nests in gravel where the median particle diameter does not exceed 10% of their fork length (Kondolf & Wolman, 1993). Thus, nest sizes and depths are positively correlated with body size (Crisp & Carling, 1989; Elliott, 1984; Gauthey et al., 2015). The depths of gravel mobilized during high flow events are influenced by the strength of the stream flow, stream gradient and substrate composition (Harrison, Legleiter, Wydzga, & Dunne, 2011). Within water courses prone to such riverbed "scour", individual scour events are likely to kill trout eggs located above the maximum scour depth, thereby exerting a strong selective pressure for a locally determined minimum female body size (Montgomery et al., 1996). Thus, due to their ability to dig deeper nests and move heavier gravel, large anadromous females may enjoy a distinct advantage over small resident females as scour depth and gravel particle size increase. This size-dependent mechanism may interfere with habitat selection in trout within a river basin,

leading to positive correlation between female body size and river size at the spawning area.

Furthermore, female brown trout show a marked preference for spawning in previously utilized nests containing incubating eggs (Gortázar, Alonso, & Jalón, 2012). This behaviour, known as redd superimposition, includes a period of excavation that leads to high mortality rates among eggs deposited by earlier spawners (McNeil, 1964; Nomoto et al., 2010). This behaviour has also been reported where brown trout and Atlantic salmon share the same spawning ground (Baglinière et al., 1979). The intensity of redd superimposition depends on the density of spawners, the size of the spawning area, the duration of the spawning period and the distribution of spawners within the river system. As with environmentally based scour, the survival of eggs depends on whether they are deposited below the depth of gravel mobility during subsequent excavations. As a result, the ability of large (i.e. anadromous) females to construct deeper nests than smaller freshwater-resident females may represent a distinct interspecific and intraspecific advantage where population density is high or where suitable spawning habitat is in short supply.

7.3 | Thermal condition and spawning phenology

In some populations, freshwater residents appear to spawn later in the spawning period than their anadromous counterparts (Jonsson & Jonsson, 1999). The asynchronous spawning of anadromous and resident females may lead to the eggs of anadromous females hatching earlier than those of resident females, potentially conferring a competitive advantage on the progeny of anadromous females through early growth opportunities. But this different temporal spawning pattern between resident and anadromous trout does not exist everywhere. In France, the spawning period of sea trout (mid-December to late January) occurs within the larger spawning period of resident trout (late November to mid-February) (J.-L. Baglinière, personal communication).

The efficiency of yolk conversion to body tissue declines as water temperature increases (Fleming & Gross, 1990), meaning that rising water temperatures during spring are likely to have a more pronounced negative impact on the growth performance of eggs spawned later in the breeding period. It is possible that the higher energy density found in the eggs of resident females relative to those of anadromous females from the same population (Jonsson & Jonsson, 1997, 1999) represents an adaptation which mitigates the competitive disadvantages that result from late spawning. Possibly, thermal differences between eggs fertilized early or late during the spawning period may also influence later growth and reproductive allocations, as they appear to do in Atlantic salmon (Finstad & Jonsson, 2012; Jonsson & Jonsson, 2014, 2018).

7.4 | Oxygen and siltation

In addition to benefitting from increased fecundity, large anadromous females, which tend to accumulate high somatic mass during marine feeding, are likely to produce larger eggs than smaller resident females (Hendry & Day, 2003; Jonsson & Jonsson, 1999). While increased redd depth is beneficial in protecting eggs from washout during scour events, the threat of egg asphyxiation due to sedimentation or weakly oxygenated water increases with burial depth (Haury, Ombredane, & Baglinière, 1999). Einum, Hendry, and Fleming (2002) found that the fitness of brown trout eggs at differing oxygen levels is size-dependant, with larger eggs exhibiting significantly higher survival than small eggs when the oxygen concentration is low, possibly as a result of their increased surface area which facilitates diffusion. Laboratory experiments with brown trout embryos suggest that sublethal stress in the gravel nest caused by hypoxia can alter the behaviour and survival of trout during the early juvenile period (Roussel, 2007). It follows that the nature of local scour regimes, dissolved oxygen levels, siltation rates and riverbed gravel composition may all influence the relative fitness and frequency of differing adult female phenotypes. These factors should select for increased body size and egg mass associated with anadromy where scour is deep, gravel particles are large, and siltation or deoxygenation represents a significant threat to egg survival.

7.5 | Male mating strategies: frequency dependence, density dependence and shelter

There is strong regional and local variation in age at maturity and freshwater residency rates of males, indicating that populations are locally adapted with regard to body size and migratory strategy (Bohlin et al., 1990; Dellefors & Faremo, 1988). Where the habitat permits, small males may safely remain close to spawning females by utilizing crevices, rocks, debris or shallow areas as refuges where the aggression of large males is avoided (Gross, 1985). Thus, the availability of appropriate refuge habitats near spawning sites may be a factor influencing the fitness and, consequently, the proportion of male brown trout that forego marine migration or mature at a small size (Jonsson & Jonsson, 2011).

While the abiotic characteristics of spawning habitat and local hydrological regimes are likely to influence the relative fitness of anadromous and freshwater-resident phenotypes in brown trout, direct competition on spawning grounds may exert density-dependent selection on these phenotypes. But also, polymorphism among mature males appears to be maintained by frequency-dependent selection during spawning that increases the relative fitness of the rarer phenotype and promotes the co-occurrence of both mating strategies (Berejikian et al., 2010; Foote et al., 1997; Gross, 1985; Hutchings & Myers, 1985). For instance, in Atlantic salmon, aggressive competition for mates between large males occupies much of their focus, allowing young and small males to go unnoticed and successfully employ their sneaking tactic when courting females. As the density of large males increases, this alternative mating behaviour may confer a greater mating success, balanced against the risk of getting killed by a large male. Conversely, the fitness of large males is likely to be reduced by competition for mates as the frequency of large males increases (Engqvist & Taborsky, 2016). Similarly, as

the frequency of precocious males increases, their individual genetic contribution is likely to diminish due to increased competition from other precocious males (Hutchings & Myers, 1994). In brown trout, males do not mature as early and small as in salmon, but the contrast between small resident and large migrant individuals provides a similar framework.

It has been argued that the development and maintenance of an evolutionarily stable alternative male reproductive strategy require a strong underlying genetic basis, although the expression of these strategies is conditional, in the sense that environmental conditions associated with growth and survival interact with genetically based threshold responses to determine individual strategy (Engqvist & Taborsky, 2016; Tomkins & Hazel, 2007). However, one cannot rule out epigenetic mechanisms, which might provide a rapid response to changing environmental conditions (Moran & Pérez-Figueroa, 2011). Hutchings and Myers (1994) suggested that within a given trout population, an evolutionarily stable continuum of strategy frequencies is maintained by polygenic thresholds (which are likely to differ significantly between sexes as well as between individuals) of environmentally controlled traits (primarily associated with growth). In this sense, the polyphenic mating strategies employed by male brown trout may be regarded as both locally adapted and phenotypically plastic, resulting from the interplay between genotype, environmental conditions and both frequency- and density-dependent pressures. While density-dependent pressures are likely to lead to high rates of migration and anadromy where feeding opportunities are poor in the home river, frequency-dependent pressures largely maintain alternative mating strategies and associated polyphenism through intrasexual competition on the spawning beds (Forseth et al., 1999; Landergren, 2005; Wysujack, Greenberg, Bergman, & Olsson, 2009).

8 | HUMAN IMPACTS ON SEA TROUT

8.1 | Climate change

Possible effects of climate change on sea trout populations have been extensively reviewed (Elliott & Elliott, 2010; Graham & Harrod, 2009; Jonsson & Jonsson, 2009a; Lassalle & Rochard, 2009). The expected climate change in the Atlantic region is for warmer, drier spring and summer seasons, and for milder and wetter winters, with more precipitation falling as rain and less as snow, shorter ice-covered periods, and more frequent periods of extreme weather, including droughts, heavy rain events and strong spates. A shorter ice-covered period may increase the activity and energy use of trout in rivers and decrease production unless feeding opportunities increase to a similar extent (Watz et al., 2015).

Climate change may also be responsible for increased rates of land erosion, which is reinforced by land-use change in agriculture and forestry practices. As a result, an increase in river sediment is likely. Suspended sediment affects trout behaviour and survival directly. Sediment loads clog gravel beds impeding brown trout from spawning and reducing recruitment success (Scheurer, Alewell, Bänninger, & Burkhardt-Holm, 2009). Invertebrate communities and growth opportunities for trout are also affected by increasing sediment input (Jones et al., 2012). An increase in water temperature, notably during the spawning period, is likely to impact reproductive behaviour and egg mortality as observed in experimental conditions in Atlantic salmon (Beall & De Gaudemar, 1999), ultimately leading to a drastic reduction in the species distribution. Overall, Jonsson and Jonsson (2009a) predicted a north and northeastward movement of the distributional range of sea trout, with decreased production and population extinction in the southern regions and invasion of new spawning and nursery rivers and feeding areas in the north.

8.2 | Fisheries

Trout are exploited through fishing both in freshwater and marine habitats. Overexploitation, that is, when a population is exploited to the extent that the optimal recruitment cannot be maintained due to a lack of spawners and thereby insufficient egg deposition, leads to population declines, and/or a shift the balance between anadromous and freshwater-resident compartments of populations. Because brown trout are iteroparous, the impact of exploitation is cumulative on older and larger fish (Solomon & Czerwinski, 2007). Catch statistics, as well as information on catch per unit effort and catch rates, are important for the monitoring of sea trout and assessments of levels of exploitation. In the Burrishoole catchment, fishing effort was found to be the most important determinant of catch with a weaker but significant relationship between catch and stock (Mills, Mahon, & Piggins, 1986). The quality of catch statistics for trout is adequate in some fisheries and countries, but needs improvement in others (Milner et al., 2007). The extent of unreported sea trout fishing is unknown, but can be significant in some countries.

8.3 | Aquaculture

Salmon farming affects sea trout by spreading infectious diseases caused by viruses, bacteria, fungi and parasites, as well as often functioning as a barrier to migration (Thorstad & Koed, 2003). Such diseases may affect both the freshwater and marine stages of the sea trout life cycle. Although numerous studies document the impact of salmon lice (see previous section on sea lice), little knowledge and monitoring are available on other effects of fish farming on wild brown trout populations (Bakke & Harris, 1998). However, considering the importance of the parasitism impact on wild salmonids in Norway, an operational salmon lice model has been developed to provide an improved monitoring system for risk assessment (Myksvoll et al., 2018) as well as the implemented "traffic light system" for a sustainable fish farming in Norway (Vollset et al., 2018). In Ireland, Single Bay Management (Anon, 2008) was implemented in the early 1990s which included close monitoring and advice to harvest or treat lice, especially in the immediate months before and during the wild smolt runs.

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8.4 | Degradation of water quality

Water acidification, pollution (e.g. from agriculture, sewage treatment works, roads and mining), hydropower developments, flow regulation, water abstraction, migratory barriers and habitat alterations as diverse as high diffuse organic load or clearing riffles of stones for passing logs through affect trout populations negatively (reviewed by Thorstad et al., 2014; Whelan & Poole, 1993).

Freshwater acidification, arising from industrial emissions of sulphur dioxide and nitrogen oxides to the atmosphere and the subsequent acid precipitation, wiped out trout populations in southern Fennoscandia during the last century. Although emissions were reduced after 1990, many rivers in this area are still affected by chronic or episodic acidification (e.g. Hesthagen et al., 2017; Kroglund et al., 2007; Rosseland & Kroglund, 2010). Brown trout are vulnerable to acidification, although to a lesser degree than Atlantic salmon (Henrikson & Brodin, 1995). Hence, it is likely that any liming strategy adopted specifically for Atlantic salmon may also restore water to a quality suitable for sea trout. However, liming strategies can still be optimized to improve conditions for sea trout in tributaries and small streams that presently are not included in the liming programme of the main stem of rivers. Furthermore, competition with more acid sensitive species than brown trout, such as Atlantic salmon, seems to increase as a consequence of liming and reduce the abundance of trout in some acidified waters treated with calcium carbonate (Hesthagen et al., 2017).

Contaminants derived from intensive agriculture, afforestation, mining and other industries impact sea trout negatively, both as a consequence of direct and indirect effects in freshwater (Jonsson, Jonsson, & Ugedal, 2011). High nitrite concentrations are lethal for embryos, this impact being higher when dissolved oxygen concentrations are low (Massa, Baglinière, Prunet, & Grimaldi, 2000). Livestock grazing contributes to river eutrophication due to runoff from livestock manure. Interestingly, intensive agriculture systems relying on a large quantity of nutrients led to an increase in productivity in River Scorff, France (Roussel et al., 2013). This coincided with an increase in growth performance in juvenile Atlantic salmon and a decrease in mean age at smolting (Rivot et al., 2009). However, this positive effect on fish may only hold within a reasonable level of eutrophication. In the Burrishoole, Ireland, land-use change was found to have no significant impact on the freshwater survival of either salmon or trout (de Eyto et al., 2016). Nevertheless, contaminants also alter the parr–smolt transformation, and influence the run timing and survival of smolts once they enter sea water (McCormick, Hansen, Quinn, & Saunders, 1998; Rosseland & Kroglund, 2010). Contaminants may damage fish gills and thereby compromise the ionoregulatory capacity of smolts (Kroglund et al., 2007; McCormick et al., 1998; Moore, Lower, Mayer, & Greenwood, 2007). Sublethal exposure to contaminants during smolting may therefore have implications for the survival for trout at sea and their tendency to migrate. Livestock trampling of stream bank may induce direct destruction of eggs and fry (Gregory & Gamett, 2009), potentially leading to population decline, as illustrated in a cutthroat trout model (Peterson, Rieman, Young, & Brammer, 2010). Stream bank trampling also increases siltation sedimentation of salmonid redds, which limits the interchange of surface and intragravel water and, therefore, the supply of dissolved oxygen to the embryo (Heywood & Walling, 2007). Stock exclusion from watercourses using riparian fencing and limited pool excavation has the potential to preserve and enhance wild trout populations in headwaters (Summers, Giles, & Stubbing, 2008). This rehabilitation work has become a widely recommended fisheries management practice (Summers, Giles, & Willis, 1996).

Road and railway activities contribute to freshwater pollution, but there is little available information on effects for trout. Meland et al. (2010) suggested that traffic-related contaminants, especially those emanating from contaminated tunnel wash water, reduce growth of juvenile trout. In winter, salt from the roads may also be an issue. In addition, poor water quality in rivers may be responsible for various skin diseases. For instance, UDN-like (Ulcerative Dermal Necrosis) disappeared from Europe in the 1970s, but in 1993, Roberts wrote: "it seems likely that UDN is a cyclical disease (…). It can therefore be expected to return again before the middle of the 21th century" (Roberts, 1993). Currently, a UDN-like disease is becoming an important driver of adult mortality in Baltic salmonids, and this disease has been detected in Latvia, Poland, Germany and Sweden (ICES, 2018).

8.5 | Threat to connectivity

Hydropower stations, dams and weirs may all comprise major obstacles to migratory trout and cause marked alteration of riverine habitats. Building of roads, railways, bridges and other installations may incur migratory barriers for sea trout. In some cases, migrations may be completely blocked, whereas in others, culverts or other constructions may not be sufficiently well-designed to enable or facilitate fish passage (Larinier, 2002). River flow regulation for irrigation, freshwater fish hatcheries, channel modification to facilitate boat traffic (e.g. locks) and the building of infrastructure along rivers all pose challenges to migratory fish like those from hydropower regulation. There are numerous studies on restoration of spawning habitats, changes in overwintering environmental conditions, fish stranding due to rapid flow decreases, migration barriers, turbine mortality and the effects of flow and temperature regimes on juvenile growth, behaviour and recruitment of trout (e.g. Aarestrup & Koed, 2003; Alonso-González, Gortázar, Sanz, & De Jalón, 2008; Pulg, Barlaup, Sternecker, Trepl, & Unfer, 2013; Saltveit, Halleraker, Arnekleiv, & Harby, 2001). Also, passages through hydrological barriers and temperature changes affect energy expenditure and decrease the fitness gain of migration. Furthermore, recent studies show that the presence of many dams negatively affects the energetic status of sea trout kelts during their seaward migration, reducing iteroparity (Haraldstad et al., 2018).

8.6 | Coastal development

There is little information on how anthropogenic factors and increased human development activity in coastal areas affect sea

trout survival and movements. It is not known how harbours, piers, bridges, fish farms, or industrial developments and deposits from mining activity in coastal areas affect sea trout. This is compounded by the construction of port facilities with piers or tethering systems that extend far offshore, as necessitated by the increasing size of ocean-going vessels. The construction of tidal power turbines is currently widely debated but the indirect impact of habitat changes associated with necessary damming and the direct impact of the spinning blades could be substantial for migratory species like trout. An increasing portion of rivers and the ocean is also now being illuminated at night. It is not known how such facilities impact sea trout, but negative effects of light pollution have been demonstrated on salmon migratory behaviour (Riley, Bendall, Ives, Edmonds, & Maxwell, 2012) and may be expected to exert the same negative effects on trout.

8.7 | Interactions among impact factors

Often, several anthropogenic factors impact trout populations simultaneously, but studies of synergistic effects of anthropogenic disturbances on fish populations are often complicated and expensive to conduct, and very few such studies on any species exist. Synergistic effects of two or more impact factors are complex, nonlinear and unpredictable, and certainly not apparent from combining knowledge of the effects of single factors studied in isolation. As one example, Finstad et al. (2012, 2007) investigated effects of salmon lice and acidification on Atlantic salmon post-smolt survival. These studies showed that smolts exposed to freshwater acidification were subsequently more vulnerable to salmon lice than were control groups held in good quality freshwater before migrating to sea. Vulnerability to salmon lice was, however, reduced if there was a recovery period following the acidification episode and prior to exposure to salmon lice. The interaction between higher temperature and reduced sea louse generation time has been implicated in exacerbating the farm lice sea trout impact (Tully, 1992) in a context of global warming. The interaction between run timing of sea trout smolts and the point in time at which those smolts gain a sea louse burden has been demonstrated to lead to additional stress on those smolts (Poole et al., 2000). Therefore, we conclude that in years when environmental conditions are less favourable for sea trout transition from freshwater to saltwater and a high abundance of sea lice is present in the area, the combined impact on trout will be greater than in more "normal" years or locations.

9 | RESEARCH QUESTIONS AND FUTURE DIRECTIONS

9.1 | Assessment of partial anadromy

In brown trout, partial anadromy is driven by complex interactions between intrinsic and extrinsic factors, leading to a wide variety of life-history patterns. In particular, partial migration is influenced by juvenile growth in freshwater, largely determined by temperature and feeding opportunities (Jonsson, 1981) and resulting in a continuum of life-history strategies in brown trout (Cucherousset et al., 2005). However, there are few empirical data sets available because studies rarely consider simultaneously sea trout and resident trout from the same population. The development of passive integrated transponder (PIT) tag monitoring programmes across Europe is promising but currently limited to small to medium coastal streams or tributaries and do rarely encompass catchment or population-level surveys. Scale samples and the relative concentrations of strontium (Sr) and calcium (Ca) in the otoliths can be used as proxies of movement of anadromous fish between freshwater and salt water. Also, investigations of nutritional status, which differs between freshwater resident and anadromous fish, or spawning ground surveys of types of spawners may offer alternative methods to study partial anadromy. In parallel, future research should explicitly incorporate both resident and anadromous individuals (and possibly all intermediate life histories), and use these in population models to improve our understanding of the complex dynamics within partly anadromous population. For instance, a recent meta-analysis highlighted that partial migration may confer a selective advantage in a stochastically varying environment (Gilroy, Gill, Butchart, Jones, & Franco, 2016). Thus, investigating whether partial anadromy under chronic global change may promote a greater resilience in the brown trout compared to other anadromous fish should be an important issue for ecologists and managers.

9.2 | Responses to climate change

By influencing metabolic rate, growth and feeding opportunities, temperature is considered a key driver of migration decisions in brown trout. With climate change, temperature tends to increase more rapidly in rivers than in the ocean, but the effect of temperature on growth opportunities depends on whether it is above or below some optimal temperature. If temperature increases above the optimal temperature for growth, we hypothesize that the degree of anadromy will increase, provided that the risk of mortality in fresh relative to marine waters remains similar. If the temperature in freshwater is below the optimal temperature for growth, freshwater residency should be favoured as the temperature increases. The latter is the case in masu salmon, where the proportion of resident fish increases with temperature increase in freshwater (Morita et al., 2014). Furthermore, flow conditions are likely to interact with temperature, by either accentuating or attenuating the impact of temperature on brown trout depending on the situation. But surely, expected changes in flow regime would increase environmental stochasticity in freshwater. As a result, we predict that the influence of climate change on anadromy rates will differ from northern to southern populations in brown trout. The flexibility of partial anadromy is an issue for future research.

Climate also influences the phenology of fish species (Anderson, Gurarie, Bracis, Burke, & Laidre, 2013; Jonsson, Jonsson, & Jonsson, 2017). In a warmer climate, eggs may hatch earlier (Alp, Erer, &

Kamalak, 2010), the length of the growth season may increase until a certain point (Elliott & Hurley, 1998), smolts should migrate earlier to sea (Jonsson & Ruud-Hansen, 1985; Otero et al., 2014), and adults return later for spawning (Alm, 1950), thereby increasing the duration of the sea sojourn. In rivers, water flow appears to influence time of freshwater entry and upstream migration, especially in small streams (Jonsson et al., 2001, 2018). Furthermore, the tendency to spend the winter at sea may increase when the sea water temperature increases (Olsen et al., 2006). The spawning period in southern populations may be prolonged as observed in Spain (Larios-López, de Figueroa, Galiana-García, Gortázar, & Alonso, 2015). Investigations of latitudinal gradients in phenological and life-history traits will help anticipate how climate change will influence sea trout in the future. However, because migratory distances to the home rivers differ, such gradient studies do not give direct evidence of changes in traits affected by migratory costs. Therefore, experimental research involving model species may also be helpful in studies of future phenology and life history of sea trout.

In a future warmer climate, age at smolting throughout much of the brown trout's distribution should decrease because of higher growth rate in freshwater; however, the opposite may be the case in the southern part of their distribution, as optimum temperature for growth will be exceeded more frequently. Whether smolt size will change or not, depends not only on growth rate, but selection for optimal size depending on size-specific mortality at sea (Jonsson et al., 2016). If mortality of small smolts increases more than that of large smolts, selection will favour larger smolts and high survival at sea, and vice versa if mortality increases most for large smolts. Furthermore, the ability to osmoregulate may be impaired at higher temperatures (McCormick, Shrimpton, Zydlewski, Wood, & McDonald, 1996) with possible full loss of anadromy in southern areas, similar to Arctic charr.

Flow conditions in rivers will change in the future climate. With increasing flow in small streams, the size of both residents, smolts as well as adult trout may increase, and vice versa if the flow decreases (Jonsson et al., 2001). Furthermore, more water may influence the relative size of males and females. Apparently, males need more water than similar sized females to be reproductively successful because of their high activity. Therefore, males may be smaller than females in small streams, and less so when stream size increases (Jonsson & Jonsson, 2015). Conversely, predicted increase in the frequency of extreme summer drought is likely to jeopardize juvenile survival and growth.

Mean male size relative to mean female size of the anadromous trout may increase towards the north (Jonsson & Jonsson, 2015). This might be because conditions in freshwater make freshwater residency less favourable in the north. However, the mechanism determining the sex ratio of freshwater resident versus anadromous trout is still unknown and open for research, as the proportion of the two varies among rivers (Table 1).

9.3 | Epigenetics

Increased winter temperature might influence embryo development, and in this century, winter temperatures are expected to increase more than summer temperatures (IPCC, 2013). Heritable variation in phenotypic plasticity suggests that although increasing temperatures are likely to affect some populations negatively, they may have the potential to adapt to changing temperature regimes (Jensen et al., 2008). The mechanism of this flexibility is, however, unknown, but appears to involve a change in gene expression, possibly caused as an epigenetic response to early thermal conditions (Jonsson & Jonsson, 2014, 2016). There is still little knowledge about epigenetic influence on phenotypically plastic traits (Jonsson & Jonsson, 2019).

9.4 | Management strategies

Stock assessments for brown trout are generally lacking across Europe. Little is known about productivity and recruitment in brown trout, as well as river-specific carrying capacities. Data are lacking to quantify the mortality induced by fisheries at sea, in freshwater and as potential by-catch. There is also lack of information on sea trout stocks regarding human impacts (e.g. aquaculture and spread of diseases and parasites, pollution and water quality, agriculture, road and railway activities). Estimates of straying among watercourses are sometimes large (Quéméré et al., 2016), but variable, possibly influenced by the size of the river and presence of lakes where trout spend the winter in a protected habitat. If straying between neighbouring populations is high, they may be managed together as meta-populations (Meier, Hansen, Bekkevold, Skaala, & Mensberg, 2011). However, in the future climate, autumn and winter precipitation may increase and thereby reduce the rate of straying with effects on the size of the management unit. As brown trout are partly anadromous, a future management programme should be coordinate with data collection programmes across Europe. To aid in its implementation, data collection suitable for supporting management of sea trout stocks should be cheap, easy and pragmatic, such as the length-based indicator (LBI) system proposed in Shephard, Davidson, Walker, and Gargan (2018).

In many countries, sea trout management is viewed as a by-product of Atlantic salmon management, and this is completely disconnected from resident trout management. Thus, there is an urgent need to develop new recommendations dedicated to brown trout ecology and plasticity to promote the conservation of this iconic species. Because trout are only partly anadromous, more research is needed to define the relative contribution of sea trout and resident trout to population dynamics, as well as more general data comparing sea survival and growth in populations across the native distribution area. Preferably, this should be done using individual tagged fish (such as PIT tagged) in order to directly couple life history to individual parameters (and avoid problems with straying, age reading, etc.). Future research should define relevant management units and provide recommendations for dedicated management actions able to account for the large plasticity in individual life-history trajectories in trout.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Aarestrup, K., Baktoft, H., Koed, A., del Villar-Guerra, D., & Thorstad, E. B. (2014). Comparison of the riverine and early marine migration behaviour and survival of wild and hatchery-reared sea trout *Salmo trutta* smolts. *Marine Ecology Progress Series*, *496*, 197–206. https://doi.org/10.3354/meps10614

Aarestrup, K., Birnie Gauvin, K., & Larsen, M. H. (2017). Another paradigm lost? Autumn downstream migration of juvenile brown trout: Evidence for a presmolt migration. *Ecology of Freshwater Fish*, *27*(1), 513–516. https://doi.org/10.1111/eff.12335

Aarestrup, K., & Jepsen, N. (1998). Spawning migration of sea trout (*Salmo trutta* (L)) in a Danish river. In J.-P. Lagardère, M.-L. Bégout Anras, & G. Claireaux (Eds.), *Advances in invertebrates and fish telemetry: Proceedings of the second conference on fish telemetry in Europe* (pp. 275–281). La Rochelle, France: Springer.

Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, *12*(3), 169–176. https://doi.org/10.1034/j.1600-0633.2003.00027.x

Aarestrup, K., Nielsen, C., & Koed, A. (2002). Net ground speed of downstream migrating radio-tagged Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) smolts in relation to environmental factors. *Hydrobiologia*, *483*(1), 95–102. https://doi.org/10.1023/A:1021306907338

Aarestrup, K., Nielsen, C., & Madsen, S. S. (2000). Relationship between gill Na+, K+-ATPase activity and downstream movement in domesticated and first-generation offspring of wild anadromous brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(10), 2086–2095. https://doi.org/10.1139/f00-164

Acolas, M.-L., Labonne, J., Baglinière, J.-L., & Roussel, J. M. (2012). The role of body size versus growth on the decision to migrate: A case study with *Salmo trutta*. *Naturwissenschaften*, *99*(1), 11–21. https://doi.org/10.1007/s00114-011-0861-5

Acolas, M.-L., Roussel, J.-M., & Baglinière, J.-L. (2008). Linking migratory patterns and diet to reproductive traits in female brown trout (*Salmo trutta* L.) by means of stable isotope analysis on ova. *Ecology of Freshwater Fish*, *17*(3), 382–393. https://doi.org/10.1111/j.1600-0633.2007.00290.x

Aldvén, D., & Davidsen, J. (2017). Marine migrations of sea trout (*Salmo trutta*). In G. Harris (Ed.), *Sea trout: Science & management: Proceedings of the 2nd international sea trout symposium* (pp. 267–276). Dundalk, Ireland: Troubador Publishing Ltd.

Aldvén, D., Hedger, R., Økland, F., Rivinoja, P., & Höjesjö, J. (2015). Migration speed, routes, and mortality rates of anadromous brown trout *Salmo trutta* during outward migration through a complex coastal habitat. *Marine Ecology Progress Series*, *541*, 151–163. https://doi.org/10.3354/meps11535

Alm, G. (1950). The sea-trout population in the Ava Stream. *Report of the Institute of Freshwater Research, Drottningholm*, *31*, 26–51.

Alonso-González, C., Gortázar, J., Sanz, D. B., & De Jalón, D. G. (2008). Dam function rules based on brown trout flow requirements: Design of environmental flow regimes in regulated streams. *Hydrobiologia*, *609*(1), 253–262. https://doi.org/10.1007/s10750-008-9408-y

Alp, A., Erer, M., & Kamalak, A. (2010). Eggs incubation, early development and growth in frys of brown trout (*Salmo trutta macrostigma*) and black sea trout (*Salmo trutta labrax*). *Turkish Journal of Fisheries and Aquatic Sciences*, *10*(3), 387–394. https://doi.org/10.4194/trjfas.2010.0312

Álvarez, D., Cano, J. M., & Nicieza, A. G. (2006). Microgeographic variation in metabolic rate and energy storage of brown trout: Countergradient selection or thermal sensitivity? *Evolutionary Ecology*, *20*(4), 345–363. https://doi.org/10.1007/s10682-006-0004-1

Anderson, J. J., Gurarie, E., Bracis, C., Burke, B. J., & Laidre, K. L. (2013). Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecological Modelling*, *264*, 83–97. https://doi.org/10.1016/j.ecolmodel.2013.03.009

Anon, (2008). *A strategy for improved pest control on Irish salmon farms* (p. 56pp). Dublin, Ireland: Department of Agriculture, Fisheries and Food.

Artemov, A. V., Mugue, N. S., Rastorguev, S. M., Zhenilo, S., Mazur, A. M., Tsygankova, S. V., … Prokhortchouk, E. B. (2017). Genome-wide DNA methylation profiling reveals epigenetic adaptation of stickleback to marine and freshwater conditions. *Molecular Biology and Evolution*, *34*(9), 2203–2213. https://doi.org/10.1093/molbev/msx156

Baerwald, M. R., Meek, M. H., Stephens, M. R., Nagarajan, R. P., Goodbla, A. M., Tomalty, K. M. H., … Nichols, K. M. (2016). Migration-related phenotypic divergence is associated with epigenetic modifications in rainbow trout. *Molecular Ecology*, *25*(8), 1785–1800. https://doi.org/10.1111/mec.13231

Bagenal, T. B. (1969). Relationship between egg size and fry survival in brown trout *Salmo trutta* L. *Journal of Fish Biology*, *1*(4), 349–353. https://doi.org/10.1111/j.1095-8649.1969.tb03882.x

Baglinière, J.-L. (1999). Introduction: The brown trout (*Salmo trutta* L)—its origin, distribution and economic and scientific significance. In J.-L. Baglinière & G. Maisse (Eds.), *Biology and ecology of the brown and sea trout* (pp. 1–12). London, UK: Springer. https://doi.org/10.1007/978-1-4471-0775-0_1

Baglinière, J.-L., & Arribe-Moutounet, D. (1985). Microrépartition des populations de truite commune (*Salmo trutta* L.) de juvenile de saumon atlantique (*Salmo salar* L.) et des autres espèces présentes dans la partie haute du Scorff (Bretagne). *Hydrobiologia*, *120*(3), 229–239. https://doi.org/10.1007/BF00045166

Baglinière, J.-L., & Champigneulle, A. (1982). Densité des populations de truite commune (*Salmo trutta* L.) et de juvéniles de saumon atlantique (*Salmo salar* L.) sur le cours principal du Scorff (Bretagne): préférendums physiques et variations annuelles (1976–1980). *Acta Oecologica: Oecologia Applicata*, *3*, 241–256.

Baglinière, J.-L., Champigneulle, A., & Nihouarn, A. (1979). La fraie du saumon atlantique (*Salmo salar* L.) et de la truite commune (*Salmo trutta* L.) sur le bassin du Scorff. *Cybium*, *3*(7), 75–96.

Baglinière, J.-L., Guyomard, R., Héland, M., Ombredane, D., & Prévost, E. (2001). Ecologie des populations de Poissons des cours d'eau à Salmonidés. In A. Neveu (Ed.), *L'eau dans l'espace rural. Vie et milieux aquatiques* (pp. 31–49). Paris, France: INRA.

Baglinière, J.-L., & Maisse, G. (1985). Precocious maturation and smoltification in wild Atlantic salmon in the Armorican massif, France. *Aquaculture*, *45*(1), 249–263. https://doi.org/10.1016/0044-8486(85)90274-1

Baglinière, J.-L., & Maisse, G. (1990). La croissance de la truite commune (*Salmo trutta* L.) sur le bassin de Scorff. *Bulletin Français de la Pêche et de la Pisciculture*, *318*, 89–101. https://doi.org/10.1051/kmae:1990012

Baglinière, J.-L., & Maisse, G. (1999). *Biology and ecology of the brown and sea trout*. Chichester, UK: Springer Praxis publishing Chichester.

Baglinière, J.-L., & Maisse, G. (2002). La biologie de la truite commune (*Salmo trutta* L.) dans la rivière Scorff, Bretagne: une synthèse des études de 1972 à 1997. *Productions Animales*, *5*(15), 319–331.

Baglinière, J.-L., Prévost, E., & Maisse, G. (1994). Comparison of population dynamics of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in a small tributary of the River Scorff (Brittany, France). *Ecology of Freshwater Fish*, *3*(1), 25–34. https://doi.org/10.1111/j.1600-0633.1994.tb00104.x

Bakke, T. A., & Harris, P. D. (1998). Diseases and parasites in wild Atlantic salmon (*Salmo salar*) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 247–266.

Bal, G., Rivot, E., Prévost, E., Piou, C., & Baglinière, J.-L. (2011). Effect of water temperature and density of juvenile salmonids on growth of young-of-the-year Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, *78*(4), 1002–1022. https://doi.org/10.1111/j.1095-8649.2011.02902.x

Balon, E. K. (1980). Early ontogeny of the North American landlocked arctic charr — sunapee *Salvelinus* (Salvelinus) *alpinus oquassa*. In E. K. Balon (Ed.), *Chaars: Salmonid fishes of the genus Salvelinus* (pp. 568–606). The Hague, Netherlands: Dr. W. Junk Publishers.

Baran, P., Delacoste, M., Lascaux, J. M., Bauba, F., & Segura, G. (1995). La compétition interspécifique entre la truite commune (*Salmo trutta* L.) et la truite arc-en-ciel (*Oncorhynchus Mykiss* Walbaum): Influence sur les modèles d'habitat. *Bulletin Français de la Pêche et de la Pisciculture*, *337–338–339*, 283–290. https://doi.org/10.1051/kmae:1995032

Bašić, T., Britton, J. R., Cove, R. J., Ibbotson, A., & Gregory, S. D. (2018). Roles of discharge and temperature in recruitment of a cold-water fish, the European grayling *Thymallus thymallus*, near its southern range limit. *Ecology of Freshwater Fish*, *27*(4), 940–951. https://doi.org/10.1111/eff.12405

Beall, E., & De Gaudemar, B. (1999). Plasticity of reproductive behaviour in Atlantic salmon *Salmo salar* (Salmonidae) in relation to environmental factors. *Cybium*, *23*(1), 9–28.

Berejikian, B. A., Van Doornik, D. M., Endicott, R. C., Hoffnagle, T. L., Tezak, E. P., Moore, M. E., & Atkins, J. (2010). Mating success of alternative male phenotypes and evidence for frequency-dependent selection in Chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(12), 1933–1941. https://doi.org/10.1139/F10-112

Berg, O. K., & Jonsson, B. (1990). Growth and survival rates of the anadromous trout, *Salmo trutta*, from the Vardnes River, northern Norway. *Environmental Biology of Fishes*, *29*(2), 145–154. https://doi.org/10.1007/BF00005031

Berglund, I. (1995). Effects of size and spring growth on sexual maturation in 1+ Atlantic salmon (*Salmo salar*) male parr: Interactions with smoltification. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(12), 2682–2694. https://doi.org/10.1139/f95-857

Bernatchez, L. (2001). The evolutionary history of brown trout (*Salmo trutta* L.) inferred from phylogeographic, nested clade, and mismatch analyses of mitochondrial DNA variation. *Evolution*, *55*(2), 351–379. https://doi.org/10.1111/j.0014-3820.2001.tb01300.x

Bird, A. (2002). DNA methylation patterns and epigenetic memory. *Genes and Development*, *16*(1), 6–21. https://doi.org/10.1101/gad.947102

Birkeland, K. (1996). Consequences of premature return by sea trout (*Salmo trutta*) infested with the salmon louse (*Lepeophtheirus salmonis* Krøyer): Migration, growth, and mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(12), 2808–2813.

Birnie Gauvin, K., & Aarestrup, K. (2018). A call for a paradigm shift: Assumed-to-be premature migrants actually yield good returns. *Ecology of Freshwater Fish*, *28*(1), 62–68. https://doi.org/10.1111/eff.12431

Blanchet, S., Loot, G., Grenouillet, G., & Brosse, S. (2007). Competitive interactions between native and exotic salmonids: A combined field and laboratory demonstration. *Ecology of Freshwater Fish*, *16*(2), 133–143. https://doi.org/10.1111/j.1600-0633.2006.00205.x

Boeuf, G., & Harache, Y. (1982). Criteria for adaptation of salmonids to high salinity seawater in France. *Aquaculture*, *28*(1), 163–176. https://doi.org/10.1016/0044-8486(82)90019-9

Bohlin, T., Dellefors, C., & Faremo, U. (1990). Large or small at maturity—Theories on the choice of alternative male strategies in anadromous salmonids. *Annales Zoologici Fennici*, *27*, 139–147. Tvärminne Zoological Station, Finland: Finnish Zoological and Botanical Publishing Board.

Bohlin, T., Pettersson, J., & Degerman, E. (2001). Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: Evidence for a migration cost. *Journal of Animal Ecology*, *70*(1), 112–121. https://doi.org/10.1046/j.1365-2656.2001.00466.x

Bordeleau, X., Davidsen, J. G., Eldøy, S. H., Sjursen, A. D., Whoriskey, F. G., & Crossin, G. T. (2018). Nutritional correlates of spatiotemporal variations in the marine habitat use of brown trout (*Salmo trutta*) veteran migrants. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*, 1744–1754. https://doi.org/10.1139/cjfas-2017-0350

Borgstrøm, R., & Heggenes, J. (1988). Smoltification of sea trout (*Salmo trutta*) at short length as an adaptation to extremely low summer stream flow. *Polskie Archwum Hydrobiologii*, *35*, 375–384.

Buffington, J. M., Montgomery, D. R., & Greenberg, H. M. (2004). Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness in mountain catchments. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(11), 2085–2096. https://doi.org/10.1139/f04-141

Byrne, C. J., Poole, R., Dillane, M., Rogan, G., & Whelan, K. F. (2004). Temporal and environmental influences on the variation in sea trout (*Salmo trutta* L.) smolt migration in the Burrishoole system in the west of Ireland from 1971 to 2000. *Fisheries Research*, *66*(1), 85–94.

Byrne, C. J., Poole, W. R., Dillane, M. G., & Whelan, K. F. (2002). The Irish sea trout enhancement programme: An assessment of the parr stocking programme into the Burrishoole catchment. *Fisheries Management and Ecology*, *9*(6), 329–341. https://doi.org/10.1046/j.1365-2400.2002.00314.x

Campbell, J. S. (1977). Spawning characteristics of brown trout and sea trout *Salmo trutta* L. in Kirk Burn, River Tweed, Scotland. *Journal of Fish Biology*, *11*(3), 217–229.

Campbell, R. N. (1979). Ferox trout, *Salmo trutta* L., and charr, *Salvelinm alpinus* (L.), in Scottish lochs. *Journal of Fish Biology*, *14*(1), 1–29. https://doi.org/10.1111/j.1095-8649.1979.tb03491.x

Champigneulle, A., Buttiker, B., Durand, P., & Melhaoui, M. (1999). Main characteristics of the biology of the trout (*Salmo trutta* L.) in Lake Léman (Lake Geneva) and some of its tributaries. In J.-L. Baglinière & G. Maisse (Eds.), *Biology and ecology of the brown and sea trout* (pp. 147–174). London, UK: Springer. https://doi.org/10.1007/978-1-4471-0775-0_6

Chapman, B. B., Hulthén, K., Brodersen, J., Nilsson, P. A., Skov, C., Hansson, L.-A., & Brönmark, C. (2012). Partial migration in fishes: Causes and consequences. *Journal of Fish Biology*, *81*(2), 456–478. https://doi.org/10.1111/j.1095-8649.2012.03342.x

Charles, K., Guyomard, R., Hoyheim, B., Ombredane, D., & Baglinière, J.-L. (2005). Lack of genetic differentiation between anadromous and resident sympatric brown trout (*Salmo trutta*) in a Normandy population. *Aquatic Living Resources*, *18*(1), 65–69. https://doi.org/10.1051/alr:2005006

Charles, K., Roussel, J.-M., Lebel, J.-M., Baglinière, J.-L., & Ombredane, D. (2006). Genetic differentiation between anadromous and freshwater resident brown trout (*Salmo trutta* L.): Insights obtained from stable isotope analysis. *Ecology of Freshwater Fish*, *15*(3), 255–263. https://doi.org/10.1111/j.1600-0633.2006.00149.x

Courter, I., Justice, C., & Cramer, S. (2009). *Flow and temperature effects on life history diversity of* Oncorhynchus mykiss *in the Yakima River basin*. Gresham, Oregon.

Crête-Lafrenière, A., Weir, L. K., & Bernatchez, L. (2012). Framing the *Salmonidae* family phylogenetic portrait: A more complete picture from increased taxon sampling. *PLoS ONE*, *7*(10), e46662. https://doi.org/10.1371/journal.pone.0046662

Crisp, D. T., & Carling, P. A. (1989). Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology*, *34*(1), 119–134. https://doi.org/10.1111/j.1095-8649.1989.tb02962.x

Cross, T. F., Mills, C. P. R., de Courcy Williams, M. (1992). An intensive study of allozyme variation in freshwater resident and anadromous trout, *Salmo trutta* L., in western Ireland. *Journal of Fish Biology*, *40*(1), 25–32. https://doi.org/10.1111/j.1095-8649.1992.tb02550.x

Cucherousset, J., Ombredane, D., Charles, K., Marchand, F., & Baglinière, J.-L. (2005). A continuum of life history tactics in a brown trout (*Salmo trutta*) population. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(7), 1600–1610. https://doi.org/10.1139/f05-057

Dahl, K. (1904). A study on trout and young salmon. *Nyt Magazin for Naturvidenskaberne*, *42*, 221–338.

Davaine, P., & Beall, E. (1997). Introduction de salmonidés en milieu vierge (Îles Kerguelen, Subantarctique): Enjeux, résultats, perspectives. *Bulletin Français de la Pêche et de la Pisciculture*, *344–345*, 93–110. https://doi.org/10.1051/kmae:1997013

Davidsen, J. G., Daverdin, M., Sjursen, A. D., Rønning, L., Arnekleiv, J. V., & Koksvik, J. I. (2014). Does reduced feeding prior to release improve the marine migration of hatchery brown trout *Salmo trutta* smolts? *Journal of Fish Biology*, *85*(6), 1992–2002. https://doi.org/10.1111/jfb.12485

Davidson, I. C., Hazlewood, M. S., & Cove, R. J. (2007). Predicted growth of juvenile trout and salmon in four rivers in England and wales based on past and possible future temperature regimes linked to climate change. In G. Harris & N. Milner (Eds.), *Sea trout: Biology, conservation and management* (pp. 401–416). https://doi.org/10.1002/9780470996027.ch28

de Eyto, E., Dalton, C., Dillane, M., Jennings, E., McGinnity, P., O'Dwyer, B., … Taylor, D. (2016). The response of North Atlantic diadromous fish to multiple stressors, including land use change: A multidecadal study. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(12), 1759–1769. https://doi.org/10.1139/cjfas-2015-0450

del Villar-Guerra, D., Aarestrup, K., Skov, C., & Koed, A. (2013). Marine migrations in anadromous brown trout (*Salmo trutta*). Fjord residency as a possible alternative in the continuum of migration to the open sea. *Ecology of Freshwater Fish*, *23*(4), 594–603. https://doi.org/10.1111/eff.12110

Dellefors, C. (1996). *Smoltification and sea migration in wild and hatchery-reared brown trout*, Salmo trutta. (Ph.D. thesis). Göteborg, Sweden: University of Göteborg.

Dellefors, C., & Faremo, U. (1988). Early sexual maturation in males of wild sea trout, *Salmo trutta* L., inhibits smoltification. *Journal of Fish Biology*, *33*(5), 741–749. https://doi.org/10.1111/j.1095-8649.1988.tb05519.x

Dieperink, C., Bak, B. D., Pedersen, L.-F., Pedersen, M. I., & Pedersen, S. (2002). Predation on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish Biology*, *61*(3), 848–852. https://doi.org/10.1111/j.1095-8649.2002.tb00917.x

Dieperink, C., Pedersen, S., & Pedersen, M. I. (2001). Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta* L.) smolts. *Ecology of Freshwater Fish*, *10*(3), 177–183. https://doi.org/10.1034/j.1600-0633.2001.100307.x

Dodson, J. J., Aubin-Horth, N., Thériault, V., & Páez, D. J. (2013). The evolutionary ecology of alternative migratory tactics in salmonid fishes. *Biological Reviews of the Cambridge Philosophical Society*, *88*(3), 602–625. https://doi.org/10.1111/brv.12019

Dominey, W. J. (1984). Alternative mating tactics and evolutionarily stable strategies. *American Zoologist*, *24*(2), 385–396. https://doi.org/10.1093/icb/24.2.385

Egglishaw, H. J., & Shackley, P. E. (1982). Influence of water depth on dispersion of juvenile salmonids, *Salmo salar* L. and *S. trutta* L., in a Scottish stream. *Journal of Fish Biology*, *21*(2), 141–155. https://doi.org/10.1111/j.1095-8649.1982.tb03995.x

Einum, S., Hendry, A. P., & Fleming, I. A. (2002). Egg-size evolution in aquatic environments: Does oxygen availability constrain size? *Proceedings of the Royal Society of London B: Biological Sciences*, *269*(1507), 2325–2330.

Eldøy, S. H., Davidsen, J. G., Thorstad, E. B., Whoriskey, F. G., Aarestrup, K., Naesje, T. F., … Arnekleiv, J. V. (2017). Marine depth use of sea trout *Salmo trutta* in fjord areas of central Norway: Marine depth use of *salmo trutta*. *Journal of Fish Biology*, *91*, 1268–1283. https://doi.org/10.1111/jfb.13463

Elliott, J. M. (1984). Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966–83. *The Journal of Animal Ecology*, *53*, 327–350. https://doi.org/10.2307/4360

Elliott, J. M. (1993). A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an English Lake District stream. *Canadian Special Publication of Fisheries and Aquatic Sciences*, *118*, 109–122.

Elliott, J. M. (1994). *Quantitative ecology and the brown trout*. Oxford, UK: Oxford University Press.

Elliott, J. M., & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: Predicting the effects of climate change. *Journal of Fish Biology*, *77*(8), 1793–1817. https://doi.org/10.1111/j.1095-8649.2010.02762.x

Elliott, J. M., & Hurley, M. A. (1998). Predicting fluctuations in the size of newly emerged sea-trout fry in a Lake District stream. *Journal of Fish Biology*, *53*(5), 1120–1133. https://doi.org/10.1111/j.1095-8649.1998.tb00468.x

Engqvist, L., & Taborsky, M. (2016). The evolution of genetic and conditional alternative reproductive tactics. *Proceedings of the Royal Society B*, *283*(1825), 20152945. https://doi.org/10.1098/rspb.2015.2945

Esteve, M. (2005). Observations of spawning behaviour in Salmoninae: *Salmo*, *Oncorhynchus* and *Salvelinus*. *Reviews in Fish Biology and Fisheries*, *15*(1–2), 1–21. https://doi.org/10.1007/s11160-005-7434-7

Euzenat, G., Fournel, F., & Fagard, J. L. (2006). Population dynamics and stock–recruitment relationship of sea trout in the River Bresle, upper Normandy, France. In G. Harris & N. Milner (Eds.), *Sea trout. Biology, conservation and management* (pp. 307–323). Cardiff, UK: Blackwell Publishing, Oxford.

Euzenat, G., Fournel, F., & Richard, A. (1999). Sea trout (*Salmo trutta* L.) in normandy and picardy. In J.-L. Baglinière, & G. Maisse (Eds.), *Biology and ecology of the brown and sea trout* (pp. 175–203). https://doi.org/10.1007/978-1-4471-0775-0_7

Evangelista, C., Boiche, A., Lecerf, A., & Cucherousset, J. (2014). Ecological opportunities and intraspecific competition alter trophic niche specialization in an opportunistic stream predator. *Journal of Animal Ecology*, *83*(5), 1025–1034. https://doi.org/10.1111/1365-2656.12208

Fahy, E. (1985). *Child of the Tides: A sea trout handbook*. Dun Laoghaire, Ireland: Glendale Press.

Fealy, R., Allot, N., Borderick, C., deEyto, E., Dillane, M., Erdil, R. M., … White, J. (2010). *RESCALE: Review and Simulate Climate and Catchment Responses at Burrishoole*. Retrieved from https://oar.marine.ie/handle/10793/31

Ferguson, A. (2004). The importance of identifying conservation units: Brown trout and Pollan biodiversity in Ireland. *Biology and*

Environment: Proceedings of the Royal Irish Academy, *104B*(3), 33–41. https://doi.org/10.3318/BIOE.2004.104.3.33

Ferguson, A. (2006). Genetics of Sea Trout, with Particular Reference to Britain and Ireland. In *Sea trout: biology, conservation and management* (pp. 155–182). https://doi.org/10.1002/9780470996027.ch12

Ferguson, A., Reed, T., Cross, T. F., McGinnity, P., & Prodöhl, P. (2019). Anadromy, potamodromy and residency in brown trout *Salmo trutta*: The role of genes and the environment. *Journal of Fish Biology*. https://doi.org/10.1111/jfb.14005

Ferguson, A., Reed, T., McGinnity, P., & Prodöhl, P. (2017). Anadromy in brown trout (*Salmo trutta*): A review of the relative roles of genes and environmental factors and the implications for management and conservation. In G. Harris (Ed.), *Sea trout: Science and management: Proceedings of the 2nd international sea trout symposium* (3–42). Leicestershire, UK: Matador.

Finstad, A. G., Forseth, T., Jonsson, B., Bellier, E., Hesthagen, T., Jensen, A. J., … Foldvik, A. (2011). Competitive exclusion along climate gradients: Energy efficiency influences the distribution of two salmonid fishes. *Global Change Biology*, *17*(4), 1703–1711. https://doi.org/10.1111/j.1365-2486.2010.02335.x

Finstad, A. G., & Jonsson, B. (2012). Effect of incubation temperature on growth performance in Atlantic salmon. *Marine Ecology Progress Series*, *454*, 75–82. https://doi.org/10.3354/meps09643

Finstad, B., & Bjørn, P. A. (2011). Present status and implications of salmon lice on wild salmonids in Norwegian coastal zones. In S. Jones & R. Beamish (Eds.), *Salmon lice: An integrated approach to understanding parasite abundance and distribution* (281–305). Chichester, UK: John Wiley & Sons.

Finstad, B., Kroglund, F., Bjørn, P. A., Nilsen, R., Pettersen, K., Rosseland, B. O., … Ebbesson, L. (2012). Salmon lice-induced mortality of Atlantic salmon postsmolts experiencing episodic acidification and recovery in freshwater. *Aquaculture*, *362*, 193–199. https://doi.org/10.1016/j.aquaculture.2010.10.037

Finstad, B., Kroglund, F., Strand, R., Stefansson, S. O., Bjørn, P. A., Rosseland, B. O., … Salbu, B. (2007). Salmon lice or suboptimal water quality—Reasons for reduced postsmolt survival? *Aquaculture*, *273*(2–3), 374–383. https://doi.org/10.1016/j.aquaculture.2007.10.019

Fjørtoft, H. B., Besnier, F., Stene, A., Nilsen, F., Bjørn, P. A., Tveten, A.-K., … Glover, K. A. (2017). The Phe362Tyr mutation conveying resistance to organophosphates occurs in high frequencies in salmon lice collected from wild salmon and trout. *Scientific Reports*, *7*(1), 14258. https://doi.org/10.1038/s41598-017-14681-6

Flaten, A. C., Davidsen, J. G., Thorstad, E. B., Whoriskey, F., Rønning, L., Sjursen, A. D., … Arnekleiv, J. V. (2016). The first months at sea: Marine migration and habitat use of sea trout *Salmo trutta* post-smolts. *Journal of Fish Biology*, *89*(3), 1624–1640. https://doi.org/10.1111/jfb.13065

Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: Ecology and evolution. *Reviews in Fish Biology and Fisheries*, *6*(4), 379–416. https://doi.org/10.1007/BF00164323

Fleming, I. A., & Gross, M. R. (1990). Latitudinal clines: A trade-off between egg number and size in Pacific salmon. *Ecology*, *71*(1), 1–11. https://doi.org/10.2307/1940241

Foote, C. J., Brown, G. S., & Wood, C. C. (1997). Spawning success of males using alternative mating tactics in sockeye salmon, *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(8), 1785–1795. https://doi.org/10.1139/f97-080

Forseth, T., & Jonsson, B. (1994). The growth and food ration of piscivorous brown trout (*Salmo trutta*). *Functional Ecology*, *8*(2), 171–177. https://doi.org/10.2307/2389900

Forseth, T., Larsson, S., Jensen, A. J., Jonsson, B., Näslund, I., & Berglund, I. (2009). Thermal growth performance of juvenile brown trout *Salmo trutta*: No support for thermal adaptation hypotheses. *Journal of Fish Biology*, *74*(1), 133–149. https://doi.org/10.1111/j.1095-8649.2008.02119.x

Forseth, T., Nesje, T. F., Jonsson, B., & Hårsaker, K. (1999). Juvenile migration in brown trout: A consequence of energetic state. *Journal of Animal Ecology*, *68*(4), 783–793. https://doi.org/10.1046/j.1365-2656.1999.00329.x

Frier, J. O. (1994). Growth of anadromaus and resident brown trout with different life histories in a danish lowland stream. *Nordic Journal of Freshwater Research*, *64*, 58–70.

Frost, W. E., & Brown, M. E. (1967). *The trout*. London, UK: HarperCollins Publishers Limited.

Fusco, G., & Minelli, A. (2010). Phenotypic plasticity in development and evolution: Facts and concepts. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1540), 547–556. https://doi.org/10.1098/rstb.2009.0267

Gargan, P. G., Poole, W. R., & Forde, G. P. (2006). A review of the status of irish sea trout stocks. In G. Harris (Ed.), *Sea trout: Science and management: Proceedings of the 2nd international sea trout symposium* (pp. 25–44). https://doi.org/10.1002/9780470996027.ch3

Gargan, P. G., Tully, O., & Poole, W. R. (2003). Relationship between sea lice infestation, sea lice production and sea trout survival in Ireland, 1992–2001. *Salmon at the Edge*, *10*, 119–135.

Gauthey, Z., Lang, M., Elosegi, A., Tentelier, C., Rives, J., & Labonne, J. (2015). Brown trout spawning habitat selection and its effects on egg survival. *Ecology of Freshwater Fish*, *26*(1), 133–140. https://doi.org/10.1111/eff.12262

Gibson, R. J., & Erkinaro, J. (2009). The influence of water depths and inter-specific interactions on cover responses of juvenile Atlantic salmon. *Ecology of Freshwater Fish*, *18*(4), 629–639. https://doi.org/10.1111/j.1600-0633.2009.00380.x

Giger, T., Excoffier, L., Day, P. J. R., Champigneulle, A., Hansen, M. M., Powell, R., & Largiadèr, C. R. (2006). Life history shapes gene expression in salmonids. *Current Biology: CB*, *16*(8), R281–282. https://doi.org/10.1016/j.cub.2006.03.053

Gilroy, J. J., Gill, J. A., Butchart, S. H., Jones, V. R., & Franco, A. M. (2016). Migratory diversity predicts population declines in birds. *Ecology Letters*, *19*(3), 308–317. https://doi.org/10.1111/ele.12569

Gortázar, J., Alonso, C., & de Jalón, D. G. (2012). Brown trout redd superimposition in relation to spawning habitat availability. *Ecology of Freshwater Fish*, *21*(2), 283–292. https://doi.org/10.1111/j.1600-0633.2011.00546.x

Gosset, C., Rives, J., & Labonne, J. (2006). Effect of habitat fragmentation on spawning migration of brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish*, *15*(3), 247–254. https://doi.org/10.1111/j.1600-0633.2006.00144.x

Graham, C. T., & Harrod, C. (2009). Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology*, *74*(6), 1143–1205. https://doi.org/10.1111/j.1095-8649.2009.02180.x

Greenberg, L., Svendsen, P., & Harby, A. (1996). Availability of microhabitats and their use by brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*). *Regulated Rivers: Research and Management*, *12*, 287–303.

Gregory, J. S., & Gamett, B. L. (2009). Cattle trampling of simulated bull trout redds. *North American Journal of Fisheries Management*, *29*(2), 361–366. https://doi.org/10.1577/M08-020.1

Gresswell, R. E., Liss, W. J., & Larson, G. L. (1994). Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(S1), 298–309.

Gross, M. R. (1985). Disruptive selection for alternative life histories in salmon. *Nature*, *313*(5997), 47–48. https://doi.org/10.1038/313047a0

Gross, M. R. (1987). Evolution of diadromy in fishes. *American Fisheries Society Symposium*, *1*, 14–25.

Gross, M. R. (1991). Evolution of alternative reproductive strategies: Frequency-dependent sexual selection in male bluegill sunfish.

Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, *332*(1262), 59–66.

Gross, M. R., Coleman, R. M., & McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science*, *239*(4845), 1291–1293. https://doi.org/10.1126/science.239.4845.1291

Halttunen, E., Gjelland, K.-Ø., Hamel, S., Serra-Llinares, R.-M., Nilsen, R., Arechavala-Lopez, P., … Finstad, B. (2018). Sea trout adapt their migratory behaviour in response to high salmon lice concentrations. *Journal of Fish Diseases*, *41*(6), 953–967. https://doi.org/10.1111/jfd.12749

Haraldstad, T., Höglund, E., Kroglund, F., Lamberg, A., Olsen, E. M., & Haugen, T. O. (2018). Condition-dependent skipped spawning in anadromous brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(12), 2313–2319. https://doi.org/10.1139/cjfas-2017-0076

Haraldstad, T., Kroglund, F., Kristensen, T., Jonsson, B., & Haugen, T. O. (2017). Diel migration pattern of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) smolts: An assessment of environmental cues. *Ecology of Freshwater Fish*, *26*(4), 541–551. https://doi.org/10.1111/eff.12298

Harris, G. (2017). *Sea Trout: Science & Management: Proceedings of the 2nd International Sea Trout Symposium*. S.l.: Matador.

Harris, G., & Milner, N. (2007). *Sea trout: Biology, conservation and management*. Oxford, UK: Wiley-Blackwell.

Harrison, L. R., Legleiter, C. J., Wydzga, M. A., & Dunne, T. (2011). Channel dynamics and habitat development in a meandering, gravel bed river. *Water Resources Research*, *47*(4), W04513. https://doi.org/10.1029/2009WR008926

Harwood, A. J., Metcalfe, N. B., Armstrong, J. D., & Griffiths, S. W. (2001). Spatial and temporal effects of interspecific competition between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in winter. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(6), 1133–1140.

Haury, J., Ombredane, D., & Baglinière, J.-L. (1999). The habitat of the brown trout (*Salmo trutta* L.) in water courses. In J.-L. Bagliniere & G. Maisse (Eds.), *Biology and ecology of the brown and sea trout* (pp. 37–89). Chichester, UK: Springer.

Hearn, W. E. (1987). Interspecific competition and habitat segregation among stream-dwelling trout and salmon: A review. *Fisheries*, *12*(5), 24–31. https://doi.org/10.1577/1548-8446(1987)012<0024:ICAHSA>2.0.CO;2

Heggberget, T. G. (1984). Habitat selection and segregation of parr of Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar* L.) in two streams in North Norway. In L. Johnson & B. L. Burns (Eds.), *Biology of the arctic charr: Proceedings of the international symposium on arctic charr, Winnipeg, Manitoba, May 1981* (pp. 217–231). Winnipeg, Canada: University of Manitoba Press.

Heggenes, J., Baglinière, J.-L., & Cunjak, R. A. (1999). Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. *Ecology of Freshwater Fish*, *8*(1), 1–21. https://doi.org/10.1111/j.1600-0633.1999.tb00048.x

Hendry, A. P., & Day, T. (2003). Revisiting the positive correlation between female size and egg size. *Evolutionary Ecology Research*, *5*(3), 421–429.

Henrikson, L., & Brodin, Y.-W. (1995). Liming of surface waters in Sweden — A synthesis. In L. Henrikson, & Y.-W. Brodin (Eds.), *Liming of acidified surface water a swedish synthesis* (pp. 1–44). https://doi.org/10.1007/978-3-642-79309-7_1

Hessle, C. (1935). Gotlands Havlaxöring. *Kungl Lantbruksstyrelsen*, *7*, 1–12.

Hesthagen, T., & Heggenes, J. (2003). Competitive habitat displacement of brown trout by Siberian sculpin: The role of size and density. *Journal of Fish Biology*, *62*(1), 222–236. https://doi.org/10.1046/j.1095-8649.2003.00024.x

Hesthagen, T., Larsen, B. M., Bolstad, G., Fiske, P., & Jonsson, B. (2017). Mitigation of acidified salmon rivers–Effects of liming on young brown trout *Salmo trutta*. *Journal of Fish Biology*, *91*(5), 1350–1364.

Heywood, M. J. T., & Walling, D. E. (2007). The sedimentation of salmonid spawning gravels in the Hampshire Avon catchment, UK: Implications for the dissolved oxygen content of intragravel water and embryo survival. *Hydrological Processes*, *21*(6), 770–788. https://doi.org/10.1002/hyp.6266

Hindar, K., Jonsson, B., Ryman, N., & Ståhl, G. (1991). Genetic relationships among landlocked, resident, and anadromous Brown Trout, *Salmo trutta* L. *Heredity*, *66*(1), 83–91. https://doi.org/10.1038/hdy.1991.11

Höjesjö, J., Stradmeyer, L., Griffiths, S., & Armstrong, J. (2010). Effects of competing brown trout on habitat use by Atlantic Salmon Parr: Controlled investigations in a laboratory stream. In P. S. Kemp (Ed.), *Salmonid fisheries: Freshwater habitat management* (pp. 194–208). https://doi.org/10.1002/9781444323337.ch9

Holmen, J., Olsen, E. M., & Vøllestad, L. A. (2003). Interspecific competition between stream-dwelling brown trout and Alpine bullhead. *Journal of Fish Biology*, *62*(6), 1312–1325. https://doi.org/10.1046/j.1095-8649.2003.00112.x

Houde, A. L. S., Wilson, C. C., & Neff, B. D. (2017). Performance of four salmonids species in competition with Atlantic salmon. *Journal of Great Lakes Research*, *43*(1), 211–215. https://doi.org/10.1016/j.jglr.2016.10.017

Hughes, M. R., Hooker, O. E., Leeuwen, T. E. V., Kettle-White, A., Thorne, A., Prodöhl, P., & Adams, C. E. (2019). Alternative routes to piscivory: Contrasting growth trajectories in brown trout (*Salmo trutta*) ecotypes exhibiting contrasting life history strategies. *Ecology of Freshwater Fish*, *28*(1), 4–10. https://doi.org/10.1111/eff.12421

Hutchings, J. A., & Myers, R. A. (1985). Mating between anadromous and nonanadromous Atlantic salmon, *Salmo salar*. *Canadian Journal of Zoology*, *63*(9), 2219–2221.

Hutchings, J. A., & Myers, R. A. (1994). The evolution of alternative mating strategies in variable environments. *Evolutionary Ecology*, *8*(3), 256–268. https://doi.org/10.1007/BF01238277

ICES. (1997). *Report of the Workshop on the Interactions between salmon lice and salmonids* (No. ICES CM 1997/M:4 Ref.:F). Edinburgh, United Kingdom, 11–15 November 1996.

ICES (2018). *Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST)* (p. 371p). Turku, Finland.

IPCC (2013). Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, … P. M. Midgley (Eds.), Cambridge, UK and New York, NY: Cambridge University Press.

Jensen, A. J., Finstad, B., Fiske, P., Hvidsten, N. A., Rikardsen, A. H., & Saksgård, L. (2012). Timing of smolt migration in sympatric populations of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(4), 711–723.

Jensen, J. L. A., & Rikardsen, A. H. (2012). Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. *Journal of Fish Biology*, *81*(2), 735–749. https://doi.org/10.1111/j.1095-8649.2012.03343.x

Jensen, K. W. (1968). Seatrout (*Salmo trutta*, L.) of the River Istra, western Norway. *Report of the Institute of Freshwater Research, Drottningholm*, *48*, 187–213.

Jensen, L. F., Hansen, M. M., Pertoldi, G., Holdensgaard, G., Mensberg, K. D., & Loeschcke, V. (2008). Local adaptation in brown trout early life-history traits: Implications for climate change adaptability. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1653), 2859–2868. https://doi.org/10.1098/rspb.2008.0870

Jepsen, N., Holthe, E., & Økland, F. (2006). Observations of predation on salmon and trout smolts in a river mouth. *Fisheries Management and Ecology*, *13*(5), 341–343. https://doi.org/10.1111/j.1365-2400.2006.00509.x

Johnsson, J. I., Rydeborg, A., & Sundström, L. F. (2004). Predation risk and the territory value of cover: An experimental study. *Behavioral*

Ecology and Sociobiology, *56*(4), 388–392. https://doi.org/10.1007/s00265-004-0791-8

Jones, D. A., Bergman, E., & Greenberg, L. (2015). Food availability in spring affects smolting in brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(11), 1694–1699. https://doi.org/10.1139/cjfas-2015-0106

Jones, J. I., Murphy, J. F., Collins, A. L., Sear, D. A., Naden, P. S., & Armitage, P. D. (2012). The impact of fine sediment on macro-invertebrates. *River Research and Applications*, *28*(8), 1055–1071. https://doi.org/10.1002/rra.1516

Jonsson, B. (1981). *Life history strategies of trout (*Salmo Trutta *L).* (PhD Thesis). Oslo, Norway: University of Oslo Oslo.

Jonsson, B. (1982). Diadromous and Resident Trout *Salmo trutta*: Is Their Difference Due to Genetics? *Oikos*, *38*(3), 297–300. https://doi.org/10.2307/3544668

Jonsson, B. (1985). Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Transactions of the American Fisheries Society*, *114*(2), 182–194. https://doi.org/10.1577/1548-8659(1985)114<182:LHPOFR>2.0.CO;2

Jonsson, B. (1989). Life history and habitat use of Norwegian brown trout (*Salmo trutta*). *Freshwater Biology*, *21*(1), 71–86. https://doi.org/10.1111/j.1365-2427.1989.tb01349.x

Jonsson, B., Jonsson, M., & Jonsson, N. (2017). Influences of migration phenology on survival are size-dependent in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology*, *95*(8), 581–587. https://doi.org/10.1139/cjz-2016-0136

Jonsson, B., & Jonsson, N. (1993). Partial migration: Niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, *3*(4), 348–365. https://doi.org/10.1007/BF00043384

Jonsson, B., & Jonsson, N. (2005). Lipid energy reserves influence life-history decision of Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in fresh water. *Ecology of Freshwater Fish*, *14*(3), 296–301. https://doi.org/10.1111/j.1600-0633.2005.00098.x

Jonsson, B., & Jonsson, N. (2006). Life-history effects of migratory costs in anadromous brown trout.*Journal of Fish Biology*, *69*(3), 860–869. https://doi.org/10.1111/j.1095-8649.2006.01160.x

Jonsson, B., & Jonsson, N. (2009a). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*(10), 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Jonsson, B., & Jonsson, N. (2009b). Migratory timing, marine survival and growth of anadromous brown trout *Salmo trutta* in the River Imsa, Norway. *Journal of Fish Biology*, *74*(3), 621–638. https://doi.org/10.1111/j.1095-8649.2008.02152.x

Jonsson, B., & Jonsson, N. (2011). *Ecology of Atlantic salmon and brown trout. Habitat as a template for life histories*. Dordrecht, Netherlands: Springer.

Jonsson, B., & Jonsson, N. (2014). Naturally and hatchery produced European trout *Salmo trutta*: Do their marine survival and dispersal differ? *Journal of Coastal Conservation*, *18*(2), 79–87. https://doi.org/10.1007/s11852-012-0224-1

Jonsson, B., & Jonsson, N. (2015). Sexual size dimorphism in anadromous brown trout *Salmo trutta*. *Journal of Fish Biology*, *87*(1), 187–193.

Jonsson, B., & Jonsson, N. (2016). Trans-generational maternal effect: Temperature influences egg size of the offspring in Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, *89*(2), 1482–1487. https://doi.org/10.1111/jfb.13040

Jonsson, B., & Jonsson, N. (2018). Egg incubation temperature affects the timing of the Atlantic salmon *Salmo salar* homing migration. *Journal of Fish Biology*, *93*(5), 1016–1020. https://doi.org/10.1111/jfb.13817

Jonsson, B., & Jonsson, N. (2019). Phenotypic plasticity and epigenetics of fish: Embryo temperature affects later developing traits. *Aquatic Biology*, *28*, 21–32.

Jonsson, B., Jonsson, N., & Albretsen, J. (2016). Environmental change influences the life history of salmon *Salmo salar* in the North Atlantic Ocean: *Salmo salar* at sea. *Journal of Fish Biology*, *88*(2), 618–637. https://doi.org/10.1111/jfb.12854

Jonsson, B., Jonsson, N., Brodtkorb, E., & Ingebrigtsen, P.-J. (2001). Life-history traits of Brown Trout vary with the size of small streams. *Functional Ecology*, *15*(3), 310–317. https://doi.org/10.1046/j.1365-2435.2001.00528.x

Jonsson, B., Jonsson, N., & Finstad, A. G. (2013). Effects of temperature and food quality on age and size at maturity in ectotherms: An experimental test with Atlantic salmon. *Journal of Animal Ecology*, *82*(1), 201–210. https://doi.org/10.1111/j.1365-2656.2012.02022.x

Jonsson, B., Jonsson, N., & Finstad, A. G. (2014). Linking embryonic temperature with adult reproductive investment in Atlantic salmon *Salmo salar*. *Marine Ecology Progress Series*, *515*, 217–226. https://doi.org/10.3354/meps11006

Jonsson, B., Jonsson, N., & Jonsson, M. (2018). Water level influences migratory patterns of anadromous brown trout in small streams. *Ecology of Freshwater Fish*, *27*(4), 1066–1075. https://doi.org/10.1111/eff.12415

Jonsson, B., Jonsson, N., & Ugedal, O. (2011). Production of juvenile salmonids in small Norwegian streams is affected by agricultural land use. *Freshwater Biology*, *56*(12), 2529–2542. https://doi.org/10.1111/j.1365-2427.2011.02678.x

Jonsson, B., & Ruud-Hansen, J. (1985). Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(3), 593–595. https://doi.org/10.1139/f85-076

Jonsson, B., & Sandlund, O. T. (1979). Environmental factors and life histories of isolated river stocks of brown trout (*Salmo trutta* m. *fario*) in Søre Osa river system, Norway. *Environmental Biology of Fishes*, *4*(1), 43–54. https://doi.org/10.1007/BF00005927

Jonsson, N., & Jonsson, B. (1997). Energy allocation in polymorphic Brown Trout. *Functional Ecology*, *11*(3), 310–317. https://doi.org/10.1046/j.1365-2435.1997.00083.x

Jonsson, N., & Jonsson, B. (1998). Body composition and energy allocation in life-history stages of brown trout. *Journal of Fish Biology*, *53*(6), 1306–1316. https://doi.org/10.1111/j.1095-8649.1998.tb00250.x

Jonsson, N., & Jonsson, B. (1999). Trade-off between egg mass and egg number in brown trout. *Journal of Fish Biology*, *55*(4), 767–783. https://doi.org/10.1111/j.1095-8649.1999.tb00716.x

Jonsson, N., & Jonsson, B. (2002). Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. *Freshwater Biology*, *47*(8), 1391–1401. https://doi.org/10.1046/j.1365-2427.2002.00873.x

Jonsson, N., Jonsson, B., & Hansen, L. P. (1994). Sea-ranching of brown trout, *Salmo trutta* L. *Fisheries Management and Ecology*, *1*(1), 67–76. https://doi.org/10.1111/j.1365-2400.1970.tb00007.x

Jonsson, N., Jonsson, B., & Hansen, L. P. (1998). Long-term study of the ecology of wild Atlantic salmon smolts in a small Norwegian river. *Journal of Fish Biology*, *52*(3), 638–650. https://doi.org/10.1111/j.1095-8649.1998.tb02023.x

Jonsson, N., Jonsson, B., Hansen, L. P., & Aass, P. (1994). Effects of seawater-acclimatization and release sites on survival of hatchery–reared brown trout *Salmo trutta*. *Journal of Fish Biology*, *44*(6), 973–981. https://doi.org/10.1111/j.1095-8649.1994.tb01269.x

Kalleberg, H. (1958). Observations in a stream tank of territoriality and competition in juvenile salmon and trout. *Report of the Institute of Freshwater Research, Drottningholm*, *39*, 55–98.

Kano, Y., Shimizu, Y., & Kondou, K. (2006). Status-dependent female mimicry in landlocked red-spotted masu salmon. *Journal of Ethology*, *24*(1), 1–7. https://doi.org/10.1007/s10164-005-0153-7

Karlström, Ö. (1977). *Habitat selection and population densities of salmon (*Salmo salar *L.) and trout (*Salmo trutta *L.) parr in Swedish rivers with some reference to human activities. Abstracts of Uppsala Dissertations from the Faculty of Science (Sweden)*, No, 404.

Keenleyside, M. H., & Dupuis, H. M. (1988). Courtship and spawning competition in pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Zoology*, *66*(1), 262–265.

Keller, I., Taverna, A., & Seehausen, O. (2011). A pyrosequencing assay for the rapid discrimination of mitochondrial lineages in the *Salmo trutta* species complex. *Molecular Ecology Resources*, *11*(1), 196–199. https://doi.org/10.1111/j.1755-0998.2010.02897.x

Kendall, N. W., McMillan, J. R., Sloat, M. R., Buehrens, T. W., Quinn, T. P., Pess, G. R., … Zabel, R. W. (2014). Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): A review of the processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(3), 319–342. https://doi.org/10.1139/cjfas-2014-0192

Kennedy, G. J. A., & Strange, C. D. (1986). The effects of intra-and inter-specific competition on the survival and growth of stocked juvenile Atlantic salmon, *Salmo solar* L., and resident trout, *Salmo trutta* L., in an upland stream. *Journal of Fish Biology*, *28*(4), 479–489.

Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*(1), 1–59.

Knudsen, C. M., Johnston, M. V., Schroder, S. L., Bosch, W. J., Fast, D. E., & Strom, C. R. (2009). Effects of passive integrated transponder tags on smolt-to-adult recruit survival, growth, and behavior of hatchery spring chinook salmon. *North American Journal of Fisheries Management*, *29*(3), 658–669. https://doi.org/10.1577/M07-020.1

Knutsen, J. A., Knutsen, H., Gjøsæter, J., & Jonsson, B. (2001). Food of anadromous brown trout at sea. *Journal of Fish Biology*, *59*(3), 533–543. https://doi.org/10.1111/j.1095-8649.2001.tb02359.x

Kondolf, G. M., & Wolman, M. G. (1993). The sizes of salmonid spawning gravels. *Water Resources Research*, *29*(7), 2275–2285. https://doi.org/10.1029/93WR00402

Kristensen, M. L., Righton, D., del Villar-Guerra, D., Baktoft, H., & Aarestrup, K. (2018). Temperature and depth preferences of adult sea trout *Salmo trutta* during the marine migration phase. *Marine Ecology Progress Series*, *599*, 209–224. https://doi.org/10.3354/meps12618

Krkošek, M., Revie, C. W., Gargan, P. G., Skilbrei, O. T., Finstad, B., & Todd, C. D. (2013). Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. *Proceedings of the Royal Society B*, *280*(1750), 20122359. https://doi.org/10.1098/rspb.2012.2359

Kroglund, F., Finstad, B., Stefansson, S. O., Nilsen, T. O., Kristensen, T., Rosseland, B. O., … Salbu, B. (2007). Exposure to moderate acid water and aluminum reduces Atlantic salmon post-smolt survival. *Aquaculture*, *273*(2), 360–373. https://doi.org/10.1016/j.aquaculture.2007.10.018

L'Abee-Lund, J. H., Jonsson, B., Jensen, A. J., Saettem, L. M., Heggberget, T. G., Johnsen, B. O., & Naesje, T. F. (1989). Latitudinal Variation in Life-History Characteristics of Sea-Run Migrant Brown Trout *Salmo trutta*. *The Journal of Animal Ecology*, *58*(2), 525. https://doi.org/10.2307/4846

Landergren, P. (2005). Survival and growth of sea trout parr in fresh and brackish water. *Journal of Fish Biology*, *58*(2), 591–593. https://doi.org/10.1111/j.1095-8649.2001.tb02275.x

Landergren, P. (2004). Factors affecting early migration of sea trout *Salmo trutta* parr to brackish water. *Fisheries Research*, *67*(3), 283–294. https://doi.org/10.1016/j.fishres.2003.10.005

Landergren, P., & Vallin, L. (1998). Spawning of sea trout, *Salmo trutta* L., in brackish waters—Lost effort or successful strategy? *Fisheries Research*, *35*(3), 229–236. https://doi.org/10.1016/S0165-7836(98)00073-3

Langeland, A., L'Abée-Lund, J. H., Jonsson, B., & Jonsson, N. (1991). Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *The Journal of Animal Ecology*, 895–912. https://doi.org/10.2307/5420

Larinier, M. (2002). Fish passage through culverts, rock weirs and estuarine obstructions. *Bulletin Français De La Pêche Et De La Pisciculture*, (364 suppl.), 119–134. https://doi.org/10.1051/kmae/2002097

Larios-López, J. E., de Figueroa, J. M. T., Galiana-García, M., Gortázar, J., & Alonso, C. (2015). Extended spawning in brown trout (*Salmo trutta*) populations from the Southern Iberian Peninsula: The role of climate variability. *Journal of Limnology*, *74*(2), 394–402. https://doi.org/10.4081/jlimnol.2015.1089

Larsson, S., Serrano, I., & Eriksson, L.-O. (2011). Effects of muscle lipid concentration on wild and hatchery brown trout (*Salmo trutta*) smolt migration. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(1), 1–12. https://doi.org/10.1139/f2011-128

Lassalle, G., & Rochard, E. (2009). Impact of twenty-first century climate change on diadromous fish spread over Europe, North Africa and the Middle East. *Global Change Biology*, *15*(5), 1072–1089. https://doi.org/10.1111/j.1365-2486.2008.01794.x

Lauridsen, R. B., Moore, A., Gregory, S. D., Beaumont, W. R. C., Privitera, L., & Kavanagh, J. A. (2017). Migration behaviour and loss rate of trout smolts in the transitional zone between freshwater and saltwater. In G. Harris (Ed.), *Sea trout: Science & management: Proceedings of the 2nd international sea trout symposium* (pp. 292–307). Leicestershire, UK: Matador.

Lecomte, F., Beall, E., Chat, J., Davaine, P., & Gaudin, P. (2013). The complete history of salmonid introductions in the Kerguelen Islands, Southern Ocean. *Polar Biology*, *36*(4), 457–475. https://doi.org/10.1007/s00300-012-1281-5

Lemopoulos, A., Uusi-Heikkilä, S., Huusko, A., Vasemägi, A., Vainikka, A., & Yi, S. (2018). Comparison of migratory and resident populations of brown trout reveals candidate genes for migration tendency. *Genome Biology and Evolution*, *10*(6), 1493–1503. https://doi.org/10.1093/gbe/evy102

Lemopoulos, A., Uusi-Heikkilä, S., Vasemägi, A., Huusko, A., Kokko, H., & Vainikka, A. (2017). Genome-wide divergence patterns support fine-scaled genetic structuring associated with migration tendency in brown trout. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(10), 1680–1692. https://doi.org/10.1139/cjfas-2017-0014

Limburg, K. E., Landergren, P., Westin, L., Elfman, M., & Kristiansson, P. (2001). Flexible modes of anadromy in Baltic sea trout: Making the most of marginal spawning streams. *Journal of Fish Biology*, *59*(3), 682–695. https://doi.org/10.1111/j.1095-8649.2001.tb02372.x

Linnaeus, C. (1758). *Systema naturae* (Vol. 1).

Lobón-Cerviá, J. (2007). Numerical changes in stream-resident brown trout (*Salmo trutta*): Uncovering the roles of density-dependent and density-independent factors across space and time. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(10), 1429–1447. https://doi.org/10.1139/f07-111

Lobón-Cerviá, J., Rasmussen, G. H., & Mortensen, E. (2017). Discharge-dependent recruitment in stream-spawning brown trout. In J. Lobón-Cerviá & N. Sanz (Eds.), *Brown trout: biology, ecology and management* (pp. 297–318). Chichester, UK: John Wiley & Sons.

Lobón-Cerviá, J., & Sanz, N. (2017). *Brown trout: Biology, ecology and management*. Chichester, UK: John Wiley & Sons.

Maisse, G., & Baglinière, J.-L. (1990). The biology of brown trout, *Salmo trutta* L., in the River Scorff, Brittany: A synthesis of studies from 1973 to 1984. *Aquaculture Research*, *21*(1), 95–106. https://doi.org/10.1111/j.1365-2109.1990.tb00385.x

Maisse, G., & Baglinière, J.-L. (1999). Biology of the brown trout (*Salmo trutta* L.) in French rivers. In J.-L. Baglinière & G. Maisse (Eds.), *Biology and ecology of the brown and sea trout* (pp. 15–35). London, UK: Springer. https://doi.org/10.1007/978-1-4471-0775-0_2

Maisse, G., Mourot, B., Breton, B., Fostier, A., Marcuzzi, O., Le Bail, P. Y., … Richard, A. (1991). Sexual maturity in sea trout, *Salmo trutta* L., running up the River Calonne (Normandy, France) at the 'finnock' stage. *Journal of Fish Biology*, *39*(5), 705–715.

Mäki-Petäys, A., Vehanen, T., & Muotka, T. (2000). Microhabitat use by age-0 brown trout and grayling: Seasonal responses to streambed restoration under different flows. *Transactions of the American Fisheries Society*, *129*(3), 771–781. https://doi.org/10.1577/1548-8659(2000)129<0771:MUBABT>2.3.CO;2

Marco-Rius, F., Caballero, P., Moran, P., & de Leaniz, C. G. (2012). And the last shall be first: Heterochrony and compensatory marine growth in sea trout (*Salmo trutta*). *PLoS ONE*, *7*(10), e45528. https://doi.org/10.1371/journal.pone.0045528

Marco-Rius, F., Caballero, P., Moran, P., & de Leaniz, C. G. (2013). Can migrants escape from density dependence? *Ecology and Evolution*, *3*(8), 2524–2534. https://doi.org/10.1002/ece3.652

Massa, F., Baglinière, J.-L., Prunet, P., & Grimaldi, C. (2000). Survie embryo-larvaire de la truite (*Salmo trutta*) et conditions chimiques dans la frayère | French Ichthyological Society - Cybium. *Cybium*, *24*(3), 129–140.

McCormick, S. D., Hansen, L. P., Quinn, T. P., & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 77–92. https://doi.org/10.1139/d98-011

McCormick, S. D., Shrimpton, J. M., & Zydlewski, J. D. (1996). Temperature effects on osmoregulatory physiology of juvenile anadromous fish. In C. M. Wood & D. G. McDonald (Eds.), *Society for experimental biology seminar series: Vol. 61. Global warming: implications for freshwater and marine fish* (pp. 279–301). New York, NY: Cambridge University Press

McKeown, N. J., Hynes, R. A., Duguid, R. A., Ferguson, A., & Prodöhl, P. A. (2010). Phylogeographic structure of brown trout *Salmo trutta* in Britain and Ireland: Glacial refugia, postglacial colonization and origins of sympatric populations. *Journal of Fish Biology*, *76*(2), 319–347. https://doi.org/10.1111/j.1095-8649.2009.02490.x

McLean, J. E., Bentzen, P., & Quinn, T. P. (2004). Does size matter? Fitness-related factors in steelhead trout determined by genetic parentage assignment. *Ecology*, *85*(11), 2979–2985. https://doi.org/10.1890/03-0488

McMillan, J. R., Katz, S. L., & Pess, G. R. (2007). Observational evidence of spatial and temporal structure in a sympatric anadromous (winter steelhead) and resident rainbow trout mating system on the Olympic Peninsula, Washington. *Transactions of the American Fisheries Society*, *136*(3), 736–748. https://doi.org/10.1577/T06-016.1

McNeil, W. J. (1964). Redd superimposition and egg capacity of pink salmon spawning beds. *Journal of the Fisheries Board of Canada*, *21*(6), 1385–1396. https://doi.org/10.1139/f64-119

Meier, K., Hansen, M. M., Bekkevold, D., Skaala, Ø., & Mensberg, K. D. (2011). An assessment of the spatial scale of local adaptation in brown trout (*Salmo trutta* L.): Footprints of selection at microsatellite DNA loci. *Heredity*, *106*(3), 488.

Meland, S., Borgstrøm, R., Heier, L. S., Rosseland, B. O., Lindholm, O., & Salbu, B. (2010). Chemical and ecological effects of contaminated tunnel wash water runoff to a small Norwegian stream. *Science of the Total Environment*, *408*(19), 4107–4117. https://doi.org/10.1016/j.scitotenv.2010.05.034

Mills, C. P. R., Mahon, G. A. T., & Piggins, D. J. (1986). Influence of stock levels, fishing effort and environmental factors on anglers' catches of Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L. *Aquaculture Research*, *17*(4), 289–297. https://doi.org/10.1111/j.1365-2109.1986.tb00116.x

Mills, C. P. R., Piggins, D. J., & Cross, T. F. (1990). *Burrishoole sea trout-a twenty year study*. 20th Annual Study Course Proceedings (pp. 61–78).

Milner, N. J., Harris, G., Gargan, P., Beveridge, M., Pawson, M. G., Walker, A., & Whelan, K. F. (2007). Perspectives on sea trout science and management. In G. Harris & N. Milner (Eds.), *Sea trout: Biology, conservation and management* (pp. 480–490). Oxford, UK: Wiley-Blackwell. https://doi.org/10.1002/9780470996027.ch34

Montgomery, D. R., Buffington, J. M., Peterson, N. P., Schuett-Hames, D., & Quinn, T. P. (1996). Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 1061–1070. https://doi.org/10.1139/f96-028

Montorio, L., Evanno, G., & Nevoux, M. (2018). Intra- and interspecific densities shape life-history traits in a salmonid population. *Oecologia*, *188*(2), 451–464. https://doi.org/10.1007/s00442-018-4213-4

Moore, A., Lower, N., Mayer, I., & Greenwood, L. (2007). The impact of a pesticide on migratory activity and olfactory function in Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture*, *273*(2), 350–359. https://doi.org/10.1016/j.aquaculture.2007.10.017

Moore, I., Dodd, J. A., Newton, M., Bean, C. W., Lindsay, I., Jarosz, P., & Adams, C. E. (2018). The influence of aquaculture unit proximity on the pattern of *Lepeophtheirus salmonis* infection of anadromous *Salmo trutta* populations on the isle of Skye, Scotland. *Journal of Fish Biology*, *92*(6), 1849–1865. https://doi.org/10.1111/jfb.13625

Moran, P., Marco-Rius, F., Megías, M., Covelo-Soto, L., & Pérez-Figueroa, A. (2013). Environmental induced methylation changes associated with seawater adaptation in brown trout. *Aquaculture*, *392–395*(Supplement C), 77–83. https://doi.org/10.1016/j.aquaculture.2013.02.006

Moran, P., & Pérez-Figueroa, A. (2011). Methylation changes associated with early maturation stages in the Atlantic salmon. *BMC Genetics*, *12*(1), 86. https://doi.org/10.1186/1471-2156-12-86

Morinville, G. R., & Rasmussen, J. B. (2003). Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(4), 401–410. https://doi.org/10.1139/f03-036

Morita, K., Fukuwaka, M., Tanimata, N., & Yamamura, O. (2010). Size-dependent thermal preferences in a pelagic fish. *Oikos*, *119*(8), 1265–1272. https://doi.org/10.1111/j.1600-0706.2009.18125.x

Morita, K., Tamate, T., Kuroki, M., & Nagasawa, T. (2014). Temperature-dependent variation in alternative migratory tactics and its implications for fitness and population dynamics in a salmonid fish. *Journal of Animal Ecology*, *83*(6), 1268–1278. https://doi.org/10.1111/1365-2656.12240

Myksvoll, M. S., Sandvik, A. D., Albretsen, J., Asplin, L., Johnsen, I. A., Karlsen, Ø., … Ådlandsvik, B. (2018). Evaluation of a national operational salmon lice monitoring system—From physics to fish. *PLoS ONE*, *13*(7), e0201338. https://doi.org/10.1371/journal.pone.0201338

Näslund, J., Sundström, L. F., & Johnsson, J. I. (2015). Autumn food restriction reduces smoltification rate, but not over-winter survival, in juvenile brown trout *Salmo trutta*. *Ecology of Freshwater Fish*, *26*(2), 205–216. https://doi.org/10.1111/eff.12268

Nielsen, C., Aarestrup, K., & Madsen, S. S. (2006). Comparison of physiological smolt status in descending and nondescending wild brown trout (*Salmo trutta*) in a Danish stream. *Ecology of Freshwater Fish*, *15*(2), 229–236. https://doi.org/10.1111/j.1600-0633.2006.00143.x

Nielsen, J. (1994). *Vandlöbsfiskenes verden – Med biologen på arbejde*. Copenhagen, Denmark: Gad.

Nika, N., Virbickas, T., & Kontautas, A. (2011). Spawning site selection and redd gravel characteristics of sea trout *Salmo trutta* in the lowland streams of Lithuania. *Oceanological and Hydrobiological Studies*, *40*(1), 46–56. https://doi.org/10.2478/s13545-011-0006-7

Nomoto, K., Omiya, H., Sugimoto, T., Akiba, K., Edo, K., & Higashi, S. (2010). Potential negative impacts of introduced rainbow trout on endangered Sakhalin taimen through redd disturbance in an agricultural stream, eastern Hokkaido. *Ecology of Freshwater Fish*, *19*(1), 116–126. https://doi.org/10.1111/j.1600-0633.2009.00396.x

Nordeng, H. (1983). Solution to the" char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*(9), 1372–1387.

Northcote, T. G. (1992). Migration and residency in stream salmonids-some ecological considerations and evolutionary consequences. *Nordic Journal of Freshwater Research. Drottningholm*, *67*, 5–17.

Økland, F., Jonsson, B., Jensen, A. J., & Hansen, L. P. (1993). Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? *Journal of Fish Biology*, *42*(4), 541–550. https://doi.org/10.1111/j.1095-8649.1993.tb00358.x

Okumuş, I., Kurtoglu, I. Z., & Atasaral, Ş. (2006). General overview of Turkish sea trout (*Salmo trutta* L.) populations. In G. Harris & N. Milner (Eds.), *Sea trout: Biology, conservation and management* (pp. 115–127. Oxford, UK: Wiley-Blackwell.

Olsen, E. M., Knutsen, H., Simonsen, J. H., Jonsson, B., & Knutsen, J. A. (2006). Seasonal variation in marine growth of sea trout, *Salmo trutta*, in coastal Skagerrak. *Ecology of Freshwater Fish*, *15*(4), 446–452. https://doi.org/10.1111/j.1600-0633.2006.00176.x

Olsén, K. H., Järvi, J. T., Mayer, I., Petersson, E., & Kroon, F. (1998). Spawning behaviour and sex hormone levels in adult and precocious brown trout (*Salmo trutta* L.) males and the effect of anosmia. *Chemoecology*, *8*(1), 9–17. https://doi.org/10.1007/PL00001803

Olsson, I. C., Greenberg, L. A., Bergman, E., & Wysujack, K. (2006). Environmentally induced migration: The importance of food. *Ecology Letters*, *9*(6), 645–651. https://doi.org/10.1111/j.1461-0248.2006.00909.x

Ombredane, D., Siegler, L., Baglinière, J.-L., & Prunet, P. (1996). Migration et smoltification des juvéniles de truite (*Salmo trutta*) dans deux cours d'eau de Basse-Normandie. *Cybium*, *20*(3), 27–42.

Otero, J., L'Abée-Lund, J. H., Castro-Santos, T., Leonardsson, K., Storvik, G. O., Jonsson, B., … Vøllestad, L. A. (2014). Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Global Change Biology*, *20*(1), 61–75. https://doi.org/10.1111/gcb.12363

Patarnello, T., Bargelloni, L., Caldara, F., & Colombo, L. (1994). Cytochrome b and 16S rRNA Sequence Variation in the *Salmo trutta* (Salmonidae, Teleostei) Species Complex. *Molecular Phylogenetics and Evolution*, *3*(1), 69–74. https://doi.org/10.1006/mpev.1994.1008

Peiman, K. S., Birnie Gauvin, K., Midwood, J. D., Larsen, M. H., Wilson, A. D. M., Aarestrup, K., & Cooke, S. J. (2017). If and when: Intrinsic differences and environmental stressors influence migration in brown trout (*Salmo trutta*). *Oecologia*, *184*(2), 375–384. https://doi.org/10.1007/s00442-017-3873-9

Petersson, E., Järvi, T., Olsén, H., Mayer, I., & Hedenskog, M. (1999). Male–male competition and female choice in brown trout. *Animal Behaviour*, *57*(4), 777–783. https://doi.org/10.1006/anbe.1998.1043

Peterson, D. P., Rieman, B. E., Young, M. K., & Brammer, J. A. (2010). Modeling predicts that redd trampling by cattle may contribute to population declines of native trout. *Ecological Applications*, *20*(4), 954–966. https://doi.org/10.1890/09-0679.1

Pettersson, J. C. E., Hansen, M. M., & Bohlin, T. (2001). Does dispersal from landlocked trout explain the coexistence of resident and migratory trout females in a small stream? *Journal of Fish Biology*, *58*(2), 487–495. https://doi.org/10.1111/j.1095-8649.2001.tb02267.x

Poole, W. R., Byrne, C. J., Dillane, M. G., Whelan, K. F., & Gargan, P. G. (2002). The Irish sea trout enhancement programme: A review of the broodstock and ova production programmes. *Fisheries Management and Ecology*, *9*(6), 315–328. https://doi.org/10.1046/j.1365-2400.2002.00315.x

Poole, W. R., & Dillane, M. G. (1998). Estimation of sperm concentration of wild and reconditioned brown trout, *Salmo trutta* L. *Aquaculture Research*, *29*(6), 439–445. https://doi.org/10.1046/j.1365-2109.1998.00223.x

Poole, W. R., Dillane, M., DeEyto, E., Rogan, G., McGinnity, P., & Whelan, K. F. (2007). Characteristics of the Burrishoole sea trout population: Census, marine survival, enhancement and stock-recruitment relationship, 1971–2003. In G. Harris & N. Milner (Eds.), *Sea trout: Biology, conservation and management* (pp. 279–306). Oxford, UK: Wiley-Blackwell. https://doi.org/10.1002/9780470996027.ch19

Poole, W. R., Nolan, D., & Tully, O. (2000). Extrapolating baseline blood cortisol levels in trout: Modelling capture effects in wild sea trout *Salmo trutta* (L.) infested with *Lepeophtheirus salmonis* (Krøyer). *Aquaculture Research*, *31*(11), 835–841.

Poole, W. R., Whelan, K. F., Dillane, M. G., Cooke, D. J., & Matthews, M. (1996). The performance of sea trout, *Salmo trutta* L., stocks from the Burrishoole system western Ireland, 1970–1994. *Fisheries Management and Ecology*, *3*(1), 73–92.

Potter, E., Campbell, R. N., Sumner, K., & Marshall, S. (2017). *Marine migrations and distribution of sea trout from rivers in Great Britain.*

Prodöhl, P., Antoniacomi, A., Bradley, C., Carlson, J., Carvalho, G. R., Coughlan, J., … Cross, T. F. (2017). Population genetics and Genetic Stock Identification of anadromous *Salmo trutta* from the Irish Sea and adjacent areas, using microsatellite DNA loci. In *Sea trout: Science and management: Proceedings of the 2nd International Sea Trout Symposium* (pp. 69–95). Retrieved from https://pure.qub.ac.uk/portal/en/publications/population-genetics-and-genetic-stock-identification-of-anadromous-salmo-trutta-from-the-irish-sea-and-adjacent-areas-using-microsatellite-dna-loci(86dedf32-1d65-4de0-80e6-4d0583fb8c85)/export.html

Prouzet, P., LeBail, P. Y., & Heydorff, M. (1984). Sex ratio and potential fecundity of Atlantic salmon (*Salmo salar* L.) caught by anglers on the Elorn River (Northern Brittany, France) during 1979 and 1980. *Aquaculture Research*, *15*(3), 123–130. https://doi.org/10.1111/j.1365-2109.1984.tb00843.x

Pulg, U., Barlaup, B. T., Sternecker, K., Trepl, L., & Unfer, G. (2013). Restoration of spawning habitats of brown trout (*Salmo trutta*) in a regulated chalk stream. *River Research and Applications*, *29*(2), 172–182.

Quéméré, E., Baglinière, J.-L., Roussel, J.-M., Evanno, G., McGinnity, P., & Launey, S. (2016). Seascape and its effect on migratory life-history strategy influences gene flow among coastal brown trout (*Salmo trutta*) populations in the English Channel. *Journal of Biogeography*, *43*(3), 498–509. https://doi.org/10.1111/jbi.12632

Quéméré, E., le Gentil, J., & Launey, S. (2011). *Analyse spatiale et temporelle des caractéristiques génétiques de la population de truite de mer de la Bresle* (Fiche Action Onema No. Rapport final; p. 124p).

Regan, C. T. (1911). *The freshwater fishes of the British Isles*. London, UK: Methuen & Co., Ltd.

Richardson, J. L., Urban, M. C., Bolnick, D. I., & Skelly, D. K. (2014). Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology and Evolution*, *29*(3), 165–176. https://doi.org/10.1016/j.tree.2014.01.002

Riley, W. D., Bendall, B., Ives, M. J., Edmonds, N. J., & Maxwell, D. L. (2012). Street lighting disrupts the diel migratory pattern of wild Atlantic salmon, *Salmo salar* L., smolts leaving their natal stream. *Aquaculture*, *330–333*, 74–81. https://doi.org/10.1016/j.aquaculture.2011.12.009

Rivot, E., Perrier, C., Jouanin, C., Roussel, J.-M., Riera, P., Porcher, J. P., & Baglinière, J.-L. (2009). Climate change may have affected growth and life history in Atlantic Salmon Juveniles over the past 30 years. *American Fisheries Society Symposium*, *69*, 855–857.

Roberts, R. J. (1993). Ulcerative dermal necrosis (UDN) in wild salmonids. *Fisheries Research*, *17*(1), 3–14. https://doi.org/10.1016/0165-7836(93)90003-P

Rohtla, M., Matetski, L., Svirgsden, R., Kesler, M., Taal, I., Saura, A., … Vetemaa, M. (2017). Do sea trout *Salmo trutta* parr surveys monitor the densities of anadromous or resident maternal origin parr, or both? *Fisheries Management and Ecology*, *24*(2), 156–162. https://doi.org/10.1111/fme.12214

Rosseland, B. O., & Kroglund, F. (2010). Lessons from acidification and pesticides. In *Atlantic salmon ecology* (pp. 387–407). https://doi.org/10.1002/9781444327755.ch15

Rounsefell, G. A. (1958). Anadromy in North American Salmonidae. *US Fish and Wildlife Service Fisheries Bulletin*, *58*, 171–185.

Roussel, J.-M. (2007). Carry-over effects in brown trout (*Salmo trutta*): Hypoxia on embryos impairs predator avoidance by alevins in experimental channels. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(5), 786–792. https://doi.org/10.1139/f07-055

Roussel, J.-M., Perrier, C., Erkinaro, J., Niemelä, E., Cunjak, R. A., Huteau, D., & Riera, P. (2013). Stable isotope analyses on archived fish scales reveal the long-term effect of nitrogen loads on carbon cycling in rivers. *Global Change Biology*, *20*(2), 523–530. https://doi.org/10.1111/gcb.12293

Rubin, J.-F., Glimsäter, C., & Jarvi, T. (2005). Spawning characteristics of the anadromous brown trout in a small Swedish

stream. *Journal of Fish Biology*, *66*(1), 107–121. https://doi.org/10.1111/j.0022-1112.2005.00586.x

Rundio, D. E., Williams, T. H., Pearse, D. E., & Lindley, S. T. (2012). Male-biased sex ratio of nonanadromous *Oncorhynchus mykiss* in a partially migratory population in California. *Ecology of Freshwater Fish*, *21*(2), 293–299. https://doi.org/10.1111/j.1600-0633.2011.00547.x

Saltveit, S. J., Halleraker, J. H., Arnekleiv, J. V., & Harby, A. (2001). Field experiments on stranding in juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) during rapid flow decreases caused by hydropeaking. *Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management*, *17*(4–5), 609–622. https://doi.org/10.1002/rrr.652

Sánchez-Hernández, J., Eloranta, A. P., Finstad, A. G., & Amundsen, P.-A. (2017). Community structure affects trophic ontogeny in a predatory fish. *Ecology and Evolution*, *7*(1), 358–367. https://doi.org/10.1002/ece3.2600

Sandlund, O. T., & Jonsson, B. (2016). Life history plasticity: Migration ceased in response to environmental change? *Ecology of Freshwater Fish*, *25*(2), 225–233. https://doi.org/10.1111/eff.12204

Sanz, N. (2017). Phylogeographic history of brown trout. In J. Lobón-Cerviá & N. Sanz (Eds.), *Brown trout: Biology, ecology and management* (pp. 15–63). Chichester, UK: John Wiley & Sons. https://doi.org/10.1002/9781119268352.ch2

Scheurer, K., Alewell, C., Bänninger, D., & Burkhardt-Holm, P. (2009). Climate and land-use changes affecting river sediment and brown trout in alpine countries—A review. *Environmental Science and Pollution Research*, *16*(2), 232–242. https://doi.org/10.1007/s11356-008-0075-3

Schram, T. A., Knutsen, J. A., Heuch, P. A., & Mo, T. A. (1998). Seasonal occurrence of *Lepeophtheirus salmonis* and *Caligus elongatus* (Copepoda: Caligidae) on sea trout (*Salmo trutta*), off southern Norway. *ICES Journal of Marine Science*, *55*(2), 163–175. https://doi.org/10.1006/jmsc.1997.0357

Scott, G. R., & Johnston, I. A. (2012). Temperature during embryonic development has persistent effects on thermal acclimation capacity in zebrafish. *Proceedings of the National Academy of Sciences*, *109*(35), 14247–14252. https://doi.org/10.1073/pnas.1205012109

Segers, F. H., & Taborsky, B. (2011). Egg size and food abundance interactively affect juvenile growth and behaviour. *Functional Ecology*, *25*(1), 166–176. https://doi.org/10.1111/j.1365-2435.2010.01790.x

Serbezov, D., Jorde, P. E., Bernatchez, L., Olsen, E. M., & Vøllestad, L. A. (2012). Life history and demographic determinants of effective/census size ratios as exemplified by brown trout (*Salmo trutta*). *Evolutionary Applications*, *5*(6), 607–618. https://doi.org/10.1111/j.1752-4571.2012.00239.x

Serbezov, D., Bernatchez, L., Olsen, E. M., & Vøllestad, L. A. (2010). Mating patterns and determinants of individual reproductive success in brown trout (*Salmo trutta*) revealed by parentage analysis of an entire stream living population. *Molecular Ecology*, *19*(15), 3193–3205. https://doi.org/10.1111/j.1365-294X.2010.04744.x

Serra-Llinares, R. M., Bjørn, P. A., Finstad, B., Nilsen, R., & Asplin, L. (2016). Nearby farms are a source of lice for wild salmonids: A reply to Jansen et al. (2016). *Aquaculture Environment Interactions*, *8*, 351–356. https://doi.org/10.3354/aei00181

Serra-Llinares, R. M., Bjørn, P. A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M., & Asplin, L. (2014). Salmon lice infection on wild salmonids in marine protected areas: An evaluation of the Norwegian 'National Salmon Fjords'. *Aquaculture Environment Interactions*, *5*(1), 1–16. https://doi.org/10.3354/aei00090

Shephard, S., Davidson, I. C., Walker, A. M., & Gargan, P. G. (2018). Length-based indicators and reference points for assessing data-poor stocks of diadromous trout *Salmo trutta*. *Fisheries Research*, *199*, 36–43. https://doi.org/10.1016/j.fishres.2017.11.024

Shephard, S., MacIntyre, C., & Gargan, P. (2016). Aquaculture and environmental drivers of salmon lice infestation and body condition in sea trout. *Aquaculture Environment Interactions*, *8*, 597–610. https://doi.org/10.3354/aei00201

Sigurjónsdóttir, H., & Gunnarsson, K. (1989). Alternative mating tactics of arctic charr, *Salvelinus alpinus*, in Thingvallavatn. *Iceland. Environmental Biology of Fishes*, *26*(3), 159–176. https://doi.org/10.1007/BF00004814

Skilbrei, O. T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F., & Strand, R. (2013). Impact of early salmon louse, *Lepeophtheirus salmonis*, infestation and differences in survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts 1997–2009. *Journal of Fish Diseases*, *36*(3), 249–260. https://doi.org/10.1111/jfd.12052

Skrochowska, S. (1969). Migration of sea trout (*Salmo trutta* L.), brown trout (*Salmo trutta m. fario* L.) and their crosses. *Polish Archiv Hydrobiologie*, *16*, 125–192.

Solomon, D. J. (1997). *Review of sea trout fecundity* (p. 22) [Technical report for the Welsh Environment Agency]. Bristol, UK: Environment Agency.

Solomon, D. J., & Czerwinski, M. (2007). Catch and release, net fishing and sea trout fisheries management. In G. Harris & N. Milner (Eds.), *Sea trout: Biology, conservation and management* (pp. 434–440). Oxford, UK: Wiley-Blackwell. https://doi.org/10.1002/9780470996027.ch30

Stradmeyer, L., Höjesjö, J., Griffiths, S. W., Gilvear, D. J., & Armstrong, J. D. (2008). Competition between brown trout and Atlantic salmon parr over pool refuges during rapid dewatering. *Journal of Fish Biology*, *72*(4), 848–860. https://doi.org/10.1111/j.1095-8649.2007.01767.x

Summers, D. W., Giles, N., & Stubbing, D. N. (2008). Rehabilitation of brown trout, *Salmo trutta*, habitat damaged by riparian grazing in an English chalkstream. *Fisheries Management and Ecology*, *15*(3), 231–240. https://doi.org/10.1111/j.1365-2400.2008.00604.x

Summers, D. W., Giles, N., & Willis, D. J. (1996). *Restoration of riverine trout habitats – A guidance manual* (R&D Technical Report W18 No. Fisheries Technical Manual 1; p. 230p). Bristol, UK: Environmental Agency.

Svärdson, G. (1966). Öringen. *Fiske*, *66*, 1–31.

Taal, I., Kesler, M., Saks, L., Rohtla, M., Verliin, A., Svirgsden, R., … Saat, T. (2014). Evidence for an autumn downstream migration of Atlantic salmon *Salmo salar* (Linnaeus) and brown trout *Salmo trutta* (Linnaeus) parr to the Baltic Sea. *Helgoland Marine Research*, *68*(2), 373–377. https://doi.org/10.1007/s10152-014-0395-2

Taal, I., Rohtla, M., Saks, L., Kesler, M., Jürgens, K., Svirgsden, R., … Vetemaa, M. (2018). Parr dispersal between streams via a marine environment: A novel mechanism behind straying for anadromous brown trout? *Ecology of Freshwater Fish*, *27*(1), 209–215. https://doi.org/10.1111/eff.12338

Tamate, T., & Maekawa, K. (2004). Female-biased mortality rate and sexual size dimorphism of migratory masu salmon, *Oncorhynchus masou*. *Ecology of Freshwater Fish*, *13*(2), 96–103. https://doi.org/10.1111/j.1600-0633.2004.00043.x

Tanguy, J. M., Ombredane, D., Baglinière, J.-L., & Prunet, P. (1994). Aspects of parr-smolt transformation in anadromous and resident forms of brown trout (*Salmo trutta*) in comparison with Atlantic salmon (*Salmo salar*). *Aquaculture*, *121*(1), 51–63. https://doi.org/10.1016/0044-8486(94)90007-8

Tappel, P. D., & Bjornn, T. C. (1983). A new method of relating size of spawning gravel to salmonid embryo survival. *North American Journal of Fisheries Management*, *3*(2), 123–135. https://doi.org/10.1577/1548-8659(1983)3<123:ANMORS>2.0.CO;2

Taranger, G. L., Karlsen, Ø., Bannister, R. J., Glover, K. A., Husa, V., Karlsbakk, E., … Svåsand, T. (2015). Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. *ICES Journal of Marine Science*, *72*(3), 997–1021. https://doi.org/10.1093/icesjms/fsu132

Thomsen, D. S., Koed, A., Nielsen, C., & Madsen, S. S. (2007). Overwintering of sea trout (*Salmo trutta*) in freshwater: Escaping

salt and low temperature or an alternate life strategy? *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(5), 793–802. https://doi.org/10.1139/f07-059

Thorpe, J. E., Metcalfe, N. B. (1998). Is smolting a positive or a negative developmental decision? *Aquaculture*, *168*(1–4), 95–103.

Thorpe, J. E., Talbot, C., & Villarreal, C. (1982). Bimodality of growth and smolting in Atlantic salmon, *Salmo salar* L. *Aquaculture*, *28*(1–2), 123–132. https://doi.org/10.1016/0044-8486(82)90015-1

Thorstad, E. B., & Finstad, B. (2018). *Impacts of salmon lice emanating from salmon farms on wild Atlantic salmon and sea trout* (NINA Report No. 1449; p. 22p). Trondheim, Norway: NINA.

Thorstad, E. B., Todd, C. D., Bjørn, P. A., Gargan, P. G., Vollset, K. W., & Halttunen, E., … Finstad, B. (2014). *Effects of salmon lice on sea trout. A literature review* (NINA Report No. 1044; p. 162p).

Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., … Finstad, B. (2015). Effects of salmon lice Lepeophtheirus salmonis on wild sea trout *Salmo trutta*—A literature review. *Aquaculture Environment Interactions*, *7*(2), 91–113. https://doi.org/10.3354/aei00142

Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., … Finstad, B. (2016). Marine life of the sea trout. *Marine Biology*, *163*(3), 47. https://doi.org/10.1007/s00227-016-2820-3

Titus, R. G., & Mosegaard, H. (1992). Fluctuating recruitment and variable life history of migratory brown trout, *Salmo trutta* L., in a small, unstable stream. *Journal of Fish Biology*, *41*(2), 239–255. https://doi.org/10.1111/j.1095-8649.1992.tb02654.x

Tomkins, J. L., & Hazel, W. (2007). The status of the conditional evolutionarily stable strategy. *Trends in Ecology and Evolution*, *22*(10), 522–528. https://doi.org/10.1016/j.tree.2007.09.002

Tully, O. (1992). Predicting infestation parameters and impacts of caligid copepods in wild and cultured fish populations. *Invertebrate Reproduction and Development*, *22*(1–3), 91–102. https://doi.org/10.1080/07924259.1992.9672261

Tully, O., Gargan, P., Poole, W. R., & Whelan, K. F. (1999). Spatial and temporal variation in the infestation of sea trout (*Salmo trutta* L.) by the caligid copepod *Lepeophtheirus salmonis* (Krøyer) in relation to sources of infection in Ireland. *Parasitology*, *119*(1), 41–51.

Tully, O., Poole, W. R., & Whelan, K. F. (1993). Infestation parameters for *Lepeophtheirus salmonis* (Kroyer)(Copepoda: Caligidae) parasitic on sea trout, *Salmo trutta* L., off the west coast of Ireland during 1990 and 1991. *Aquaculture Research*, *24*(4), 545–555.

Tully, O., Poole, W. R., Whelan, K. F., & Merigoux, S. (1993). Parameters and possible causes of epizootics of *Lepeophtheirus salmonis* (Krøyer) infesting sea trout (*Salmo trutta* L.) off the west coast of Ireland. In G. A. Boxshall & D. Defaye (Eds.), *Pathogens of wild and farmed fish: Sea lice* (pp. 202–213). Chichester, UK: Ellis Horwood Limited

Tully, O., & Whelan, K. F. (1993). Production of nauplii of *Lepeophtheirus salmonis* (Krøyer)(Copepoda: Caligidae) from farmed and wild salmon and its relation to the infestation of wild sea trout (*Salmo trutta* L.) off the west coast of Ireland in 1991. *Fisheries Research*, *17*(1–2), 187–200.

Van Doornik, D. M., Berejikian, B. A., & Campbell, L. A. (2013). Gene flow between sympatric life history forms of *Oncorhynchus mykiss* located above and below migratory barriers. *PLoS ONE*, *8*(11), e79931. https://doi.org/10.1371/journal.pone.0079931

Vøllestad, L. A. (2017). In I. J. Lobón-Cerviá & N. Sanz (Eds.), *Brown Trout* (pp. G1–G72). https://doi.org/10.1002/9781119268352.app

Vollset, K. W., Dohoo, I., Karlsen, Ø., Halttunen, E., Kvamme, B. O., Finstad, B., … Barlaup, B. T. (2018). Disentangling the role of sea lice on the marine survival of Atlantic salmon. *ICES Journal of Marine Science*, *75*(1), 50–60. https://doi.org/10.1093/icesjms/fsx104

Vollset, K. W., Krontveit, R. I., Jansen, P. A., Finstad, B., Barlaup, B. T., Skilbrei, O. T., … Dohoo, I. (2016). Impacts of parasites on marine survival of Atlantic salmon: A meta-analysis. *Fish and Fisheries*, *17*(3), 714–730. https://doi.org/10.1111/faf.12141

Walker, A. M., & Bayliss, B. D. (2007). The spawning habitat requirements of sea trout: A multi-scale approach. In G. Harris & N. Milner (Eds.), *Sea trout: Biology, conservation and management* (pp. 325–341). Oxford, UK: Wiley-Blackwell. https://doi.org/10.1002/9780470996027.ch21

Watz, J., Bergman, E., Calles, O., Enefalk, A., Gustafsson, S., Hagelin, A., … Jonsson, B. (2015). Ice cover alters the behavior and stress level of brown trout *Salmo trutta*. *Behavioral Ecology*, *26*(3), 820–827. https://doi.org/10.1093/beheco/arv019

Wells, A., Grierson, C. E., MacKenzie, M., Russon, I. J., Reinardy, H., Middlemiss, C., … Hazon, N. (2006). Physiological effects of simultaneous, abrupt seawater entry and sea lice (*Lepeophtheirus salmonis*) infestation of wild, sea-run brown trout (*Salmo trutta*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(12), 2809–2821. https://doi.org/10.1139/f06-160

Wells, A., Grierson, C. E., Marshall, L., MacKenzie, M., Russon, I. J., Reinardy, H., … Hazon, N. (2007). Physiological consequences of "premature freshwater return" for wild sea-run brown trout (*Salmo trutta*) postsmolts infested with sea lice (*Lepeophtheirus salmonis*). *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(10), 1360–1369. https://doi.org/10.1139/f07-107

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, *15*, 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141

Whelan, K. F. (1989). *The angler in Ireland: Game, coarse & sea*. Dublin, Ireland: Country House.

Whelan, K. F., & Poole, W. R. (1993). The sea trout stock collapse, 1989–1992. In J. D. Reynolds (Ed.), *The conservation of aquatic systems: Proceedings of a seminar Held on 18–19 February 1993* (pp. 101–110). Dublin, Ireland: Royal Irish Academy

Winter, E. R., Tummers, J. S., Aarestrup, K., Baktoft, H., & Lucas, M. C. (2016). Investigating the phenology of seaward migration of juvenile brown trout (*Salmo trutta*) in two European populations. *Hydrobiologia*, *775*(1), 139–151. https://doi.org/10.1007/s10750-016-2720-z

Wysujack, K., Greenberg, L. A., Bergman, E., & Olsson, I. C. (2009). The role of the environment in partial migration: Food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. *Ecology of Freshwater Fish*, *18*(1), 52–59. https://doi.org/10.1111/j.1600-0633.2008.00322.x

Young, K. A. (2005). Life–history variation and allometry for sexual size dimorphism in Pacific salmon and trout. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*(1559), 167–172.

Závorka, L., Koeck, B., Cucherousset, J., Brijs, J., Näslund, J., Aldvén, D., … Johnsson, J. I. (2017). Co-existence with non-native brook trout breaks down the integration of phenotypic traits in brown trout parr. *Functional Ecology*, *31*(8), 1582–1591. https://doi.org/10.1111/1365-2435.12862

Zimmerman, C. E., & Reeves, G. H. (2000). Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: Evidence from spawning surveys and otolith microchemistry. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(10), 2152–2162.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Environmental influences on life history strategies in partially anadromous brown trout (Salmo trutta, Salmonidae)

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Characterisation of salmonid food webs in the rivers and lakes of an Irish peatland ecosystem

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CHARACTERISATION OF SALMONID FOOD WEBS IN THE RIVERS AND LAKES OF AN IRISH PEATLAND ECOSYSTEM

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ABSTRACT

Peatlands are being degraded by the combined impacts of land use and climate change. Carbon stored in peat is a key constituent of aquatic food webs in rivers and lakes of humic catchments, and changes in the downstream transport of this allochthonous carbon may have considerable implications for the production of Atlantic salmon and brown trout. Understanding the food web of these keystone species is therefore crucial to their conservation in a changing world. Here, we use a combination of stomach content analysis (SCA) and stable isotope analysis (SIA) to characterise the diet of juvenile salmonids in aquatic habitats of a typical Irish peatland catchment (Burrishoole). SCA showed that Diptera, Ephemeroptera, Plecoptera and Trichoptera were the main components of the diet of juvenile salmonids. *Daphnia* were the primary prey item in salmon smolt stomachs. The average stable isotope signature of salmonids was 9.26 ± 0.87‰ δ^{15}N and -25.6 ± 1.99‰ δ^{13}C, but differed between species, age class and habitat (river vs lake). Salmonids were supported by a wide range of carbon energy sources, with δ^{13}C increasing as fish moved downstream out of the headwater rivers and into a large downstream lake.

INTRODUCTION

Peatlands occupy approximately 20% or 14,000km^2 of the land area of Ireland (Connolly and Holden 2009), holding up to 75% of national soil carbon stocks (Renou-Wilson *et al.* 2011). Healthy peatlands provide a wide range of ecosystem services, including carbon storage, climate regulation, biodiversity support, water filtration and supply, and hydrological control (Bonn *et al.* 2009). The waters draining peatlands underpin many of these services, and the ecological quality of the rivers and lakes in peatland catchments are crucial to the functional integrity of peatlands as a whole. The rivers and streams draining peatlands are important conduits linking terrestrial and oceanic ecosystems by transporting soil organic carbon from land to sea (Asmala, Carstensen and Räike 2019). It is widely acknowledged that peatlands and their aquatic ecosystems are especially sensitive to climate change (Ise *et al.* 2008), and that resultant changes in these important long-term stores are occurring. For example, increases in organic carbon (OC) concentrations has already been reported in many aquatic peatland ecosystems in the Northern Hemisphere (Freeman *et al.* 2001; Jennings *et al.* 2010; Couture, Houle and Gagnon 2012; Asmala *et al.* 2019).

Salmonids (Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L.) and European eel (*Anguilla anguilla* L.) are keystone native species in the aquatic habitats of peatland catchments spanning the Atlantic seaboard of western Europe. These species exert considerable top down control on all aspects of the ecology of rivers and lakes in these catchments (O'Gorman, Lantry and Schneider 2004; Layer *et al.* 2011). Terrestrial (allochthonous) support of aquatic food webs, such as pulses of organic matter (both particulate and dissolved) can be significant (e.g. Solomon *et al.* 2011; Bartels *et al.* 2012; Wilkinson *et al.* 2013), meaning that changes such as peatland degradation or increased afforestation can have significant implications for the production of juvenile fish (Tanentzap *et al.* 2014).

It is currently unknown how changes in the terrestrial carbon cycling in peatlands will affect the production of salmon and trout, although recent work indicates that it is likely to be a complex response (Finstad *et al.* 2014). In addition, the role that salmonids have on controlling carbon cycling through river and lakes has yet to be determined. Recent research has quantified the role that marine fish populations have on the carbon cycle of oceanic waters (Trueman *et al.* 2014), where it was estimated that benthopelagic fishes from the

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UK-Irish continental slope capture and store a volume of carbon equivalent to over 1 million tonnes of CO^2 every year. It is possible that the freshwater fish of peatland habitats can exert a similar influence, but the magnitude of the transfer of carbon to fish biomass along the LOAC (land-ocean-aquatic continuum) is, as yet, unknown. The Burrishoole catchment on the western seaboard of Ireland is an internationally important index site for diadromous fish monitoring, with long-term records of salmon, trout and eel densities and migration (Poole *et al*., 2006, 2018; McGinnity *et al*. 2009; de Eyto *et al*. 2016a). Over the last 20 years, considerable progress has been made on resolving the carbon cycle of the aquatic ecosystems in the catchment through the use of the long-term environmental monitoring data. It has already been shown that the supply of allochthonous carbon to surface waters is largely determined by hydrological and meteorological factors (discharge, air temperature) (Ryder *et al*. 2014; Doyle *et al*. 2019), which are projected to change as climate change accelerates (Fealy *et al*. 2014). This is predicted to result in larger exports of organic carbon from peat to rivers and lakes (Jennings *et al*. 2010). Palaeolimnological investigations of the two largest freshwater lakes in the catchment (Feeagh and Bunaveela) have revealed a changing aquatic environment, primarily related to land use changes in the second half of the twentieth century (Dalton *et al*. 2014). Commercial coniferous forestry was established from the 1950s and currently covers 23% of the catchment area. In addition, sheep numbers in the catchment increased rapidly from about 500 in the 1970s to a high of ~10,000 by 2000, before decreasing as a result of destocking incentives. Organic matter (% LOI: loss on ignition) fluctuated throughout sediment cores taken from the lakes, but increased in the second half of the century, coincident with increased erosion of upland peats. Increases in levels of %C (~10 to 20) and $\delta^{15}N$ (<2 to 2.5‰) in the sediments of Feeagh coincided with organic matter increases and are within the range characteristic of terrestrial plants, and ratios of C:N greater than twenty indicated a predominantly terrestrial source for organic matter (Meyers 2003). These land use changes manifested as increased erosion of peat, increased export of sediment into the lakes and a reduction in water clarity (Sparber 2012). Biological communities in Lough Feeagh (diatoms and cladocerans) have been impacted by these changes (Dalton *et al*. 2014), and we know that the pelagic communities in Lough Feeagh are currently primarily supported by allochthonous carbon at specific times in the year (Ryder 2015).

There is, therefore, much evidence to suggest that the aquatic food webs of Burrishoole are dependent on, or influenced by, terrestrial allochthonous sources, and that this influence may have increased over the last six decades. This influence is likely to increase further as peatlands destabilise with climate warming (Jones, Donnelly and Albanito 2006; Gallego-Sala *et al*. 2010). However, a current gap in our knowledge is the role that fish play in the aquatic food web, and to what extent their production is determined by carbon sources. A first step in filling this gap is to fully characterise the food web of the rivers and lakes in Burrishoole, which is the aim of this study. Stable isotope analysis (SIA) and stomach content analysis (SCA) were carried out on the same fish samples, with the aim of cataloguing and understanding how the feeding ecology of salmonids in Burrishoole varies with species (salmon and trout), age class (0+, 1+ and smolt) and habitat (river, littoral lake and pelagic lake) over the short (days) to medium (months) term. SCA was used to provide a snapshot of the diet of fish at a given time and inform the SIA. Shifts in diet along the headwater to sea gradient were also inferred from the SIA, along with the trophic position of invertebrates and fish. In conducting this study, we wish to provide a baseline against which future changes can be assessed, and background for the design of studies with more specific research questions.

MATERIAL AND METHODS

Burrishoole is a small (100km^2) upland catchment (53° 56' N, 9° 35' W) draining into the North-east Atlantic through Clew Bay (Fig. 1). Climatically influenced by the Atlantic Ocean (Jennings *et al*., 2000; Allott, McGinnity and O'Hea, 2005; Blenckner *et al*., 2007), the catchment experiences a temperate, oceanic climate with mild winters and relatively cool summers. Maximum summer air temperatures rarely exceed 20°C, while minimum winter temperatures are usually between 2°C and 4°C. The base geology on the western side of the catchment is predominantly quartzite and schist, leading to acidic runoff with poor buffering capacity. By comparison, the geology on the eastern side is more complex as quartzite and schist are interspersed with veins of volcanic rock, dolomite and wacke, leading to higher buffering capacity and aquatic production. Soils in the catchment comprise poorly drained gleys, peaty podzols and blanket peats. Lough Feeagh is the largest freshwater lake in the catchment (Surface area = 4km^2, maximum depth = 45m), and is oligotrophic (total phosphorous <10 $\mu g\ l^{-1}$), highly coloured (*c*. 80mg l^{-1} PtCo) due to high levels of dissolved organic carbon (DOC), and slightly acidic (pH = *c*. 6.7) with low alkalinity (<20mgl^{-1} $CaCO_3$) (de Eyto *et al*. 2016b).

BIOLOGICAL ANALYSIS

Samples for isotopic determination were collected concurrently around Lough Feeagh in 2015 and

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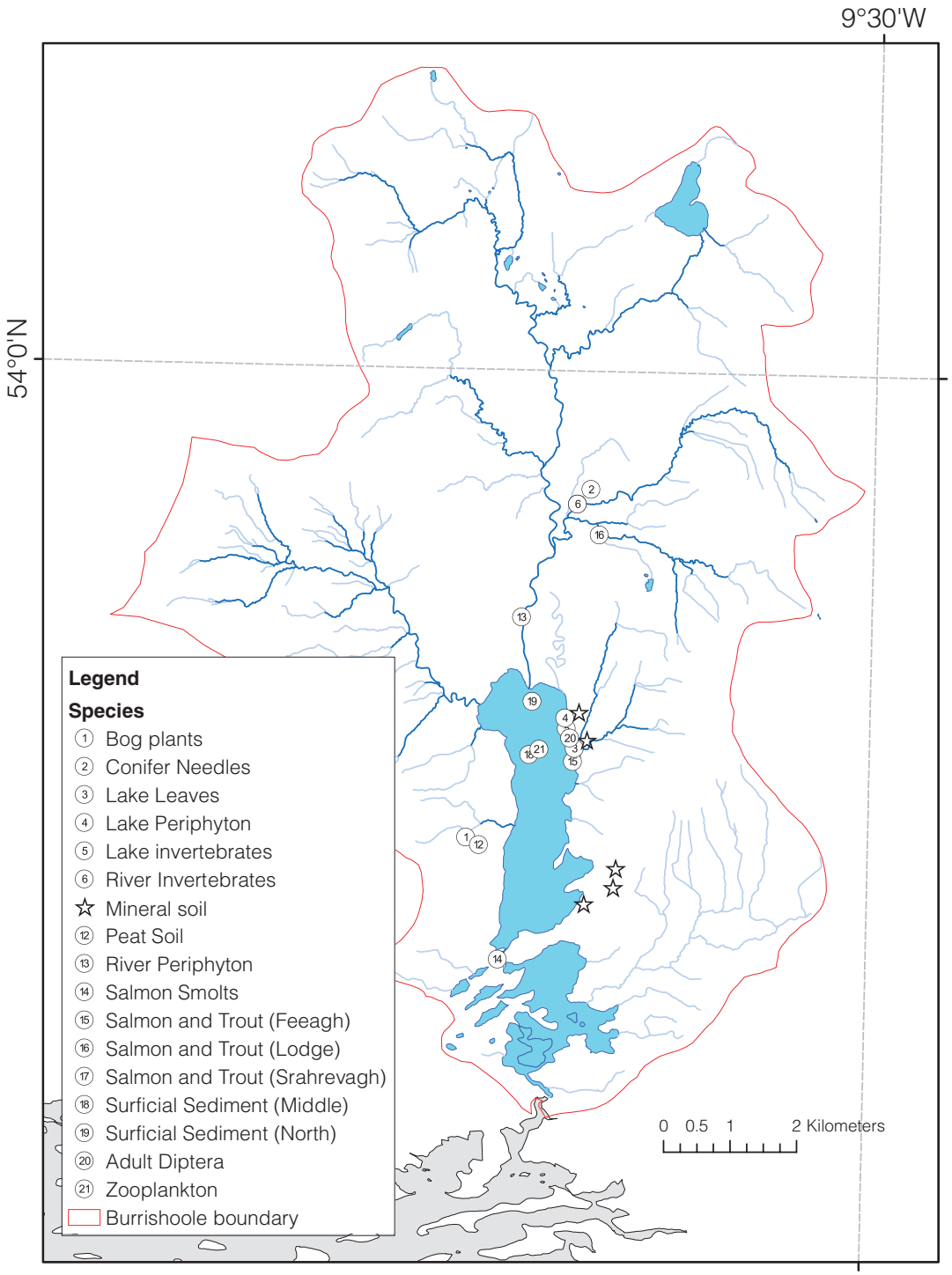


Figure 1—Map showing the location of samples collected in and adjacent to Lough Feeagh for stable isotope analysis.

2016 (Fig. 1) according to methods described below (and listed in Table 1) and following techniques described in Solomon *et al.* (2011), Karlsson *et al.* (2012) and Tanentzap *et al.* (2014). All samples were dried in an oven for 24 hours at 50°C, then crushed to a fine powder in a pestle and mortar, and weighed into individual pre-weighed tin cups.

Five samples of peat soils were collected on Lettermaghera bog (Fig. 1) in October 2015 using a plastic corer. Cores were taken from bare peat only.

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Table 1—Samples collected for Stable Isotope Analysis including number of individuals, location and date of sampling

	Sampling method	*Number of samples*	*Location (Fig 1)*	*Date*
Consumer				
Lake Trout (0+)	Draft net	10	15	7 Oct 2015
Lake Trout (1+)	Draft net	10	15	7 Oct 2015
Lake Salmon (0+)	Draft net	10	15	7 Oct 2015
Lake Salmon (1+)	Draft net	10	15	7 Oct 2015
River Trout (0+)	Electrofishing	5	16 and 17	12 Oct 2016
River Trout (1+)	Electrofishing	5	16 and 17	12 Oct 2016
River Salmon (0+)	Electrofishing	5	16 and 17	12 Oct 2016
River Salmon (1+)	Electrofishing	5	16 and 17	12 Oct 2016
Migrating Salmon (smolts)	Lake Outflow Trap	20	14	3-25 May 2016
Source				
Terrestrial				
Peat	Cores	5	12	19 Oct 2015
Lake leaves	Hand collection	5	3	19 Oct 2015
Mineral Soils	Cores	5	*	19 Jan 2015
Bog plants	Hand picked	5	1	19 Oct 2015
Conifer needles	Hand picked	5	2	19 Oct 2015
Diptera (adult flies)	Hand picked	4	20	31 Oct 2016
Pelagic				
Zooplankton (*Daphnia* sp.)	Vertical haul	3	21	19 Oct 2015
Zooplankton (Cyclopoid sp.)	Vertical haul	3	21	19 Oct 2015
Benthic				
River periphyton	Scrapped off rocks	5	13	19 Oct 2015
Lake periphyton	Tiles	5	4	19 Oct 2015
Lake invertebrates (*Gammarus duebenii*)	Sweep net	3	5	19 Oct 2015
Lake invertebrates (*Heptagenia* sp.)	Sweep net	5	5	19 Oct 2015
River invertebrates (Mayfly sp.)	Sweep net	3	6	27 Oct 2016
Profundal				
Surficial sediment	Sediment traps	5	18 and 19	19 Oct 2015

Mineral soils were collected at five separate locations on the eastern side of Lough Feeagh. The chosen soil samples represent a range of mineral soils that occur in the lake catchment. The mineral soils sampled were mostly podzols with strongly stratified horizons. The mineral soils were sampled at locations shown in Fig. 1. Surficial lake sediment was taken from traps in the north and centre of Lough Feeagh, which were in place between 15 June and 20 October 2015. Sediment from five traps was emptied into separate bottles. A subsample of each bottle was filtered through GF/F filter paper and the filtered solid used for analysis.

Terrestrial primary producers (leaves) were sampled in October 2015. Representative bog plants were sampled by selecting fresh (growing) vegetation from hummocks on Lettermaghera bog (Fig. 1). The leaves and young branches of *Calluna vulgaris* (L.) Hull, *Molinia caerulea* (L.) Moench and *Sphagnum* spp. were cut and put into a zip lock bag. Conifer needles were cut directly from a stand of *Pinus contorta* Douglas ex Loudon conifers adjacent to the Srahrevagh river. In addition, decomposing leaf litter was collected from dead leaves floating in the littoral area of Lough Feeagh. Leaves were mostly from *Fraxinus* (L.), *Salix* (L.), *Betula* (L.), and *Quercus* (L.) species. All samples were cut into small pieces for processing.

Five samples of river periphyton were collected from the Black River (Fig. 1) in October 2015. One rock submerged in the river channel was chosen per sample. Each rock was placed in a white tray, scrubbed with a tooth brush and washed with distilled water. The water from each sample was stored in a pre-washed separate bottle. In the laboratory each of the five samples was filtered thorough GF/F filers and the filtered solid used for analysis. Lake periphyton was sampled from tiles were placed in

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the littoral zone of Lough Feeagh in on 5 August 2015 and removed on 20 October 2015. Each tile was scrubbed with a toothbrush and rinsed with distilled water into a separate pre-washed bottle. In the laboratory each sample was filtered through GF/F filter paper and oven-dried. Following drying it was discovered that the required mass of material could not be scraped off the filters for analysis. Instead, several cores of each sample were taken from each of the filter papers and weighed into a pre-weighed tin cup. Cores were also cut from unused, dried filters and an average weight was measured (N = 10). The mass of each lake periphyton sample were calculated as:

(Mass of sample + core) –
(Average mass of unused core) = Mass of sample

Zooplankton were sampled in October 2015 using a vertical haul through the water column from 20m with a conical zooplankton net (53µm mesh). 100 individual cyclopoid copepods, calanoid copepods and *Daphnia* sp. were counted into beakers containing filtered lake water and left overnight to allow their guts to evacuate. Three samples of each group (nine beakers in total) were prepared. Each sample was then washed with deionised water and placed in porcelain crucibles for processing.

A kick-sample net was used to sample benthic invertebrates in the lake littoral region in October 2015. Individuals of *Gammarus duebenii celticus* Stock and Pinkster 1970 and *Heptagenia* sp. Walsh, 1863 were picked out by hand and left in filtered lake water overnight for them to expel their gut contents. For *Heptagenia* (mayfly), ten individuals were considered as a sample. Five *Gammarus* individuals were considered a sample. River invertebrates (a mix of three may fly species, *Baetis rhodani* (Pictet 1843), *Heptagenia* sp. and *Rhithrogenia semicolorata* (Curtis 1834)) were similarly sampled and processed. Winged (adult) Diptera were sampled by handpicking them from the lake shore as they were caught in spider webs suspended at approximately 1 metre height. Five to ten flies were grouped for a sample, and four samples were collected.

Littoral lake samples of salmon and trout (+0 and +1) were caught in a draft net in October 2015 (Fig. 1). River samples of salmon and trout (+0 and +1) were caught by electrofishing in October 2016 from two upland rivers above Lough Feeagh (the Lodge and Srahrevagh river). Salmon smolts (2+) were sampled as they migrated downstream through fish traps at the seaward end of Lough Feeagh during the smolt run of May 2016 and these were classified as having come from pelagic lake habitat. Fish sample sizes are given in Table 1. As the trout population of Burrishoole is primarily resident (i.e. non-anadromous), only 0+ and 1+ fish were sampled for this study, both from river and littoral lake habitats (Table 2). The fish were immediately stored in a freezer (-18 °C) until the time of dissection. The fish were later (within 3 months of being caught) defrosted and their digestive tracts removed. A sample of white flesh was removed from each fish and care was taken to avoid bone, skin, scales and other non-muscle material. The stomach content of each fish was dissected, and the occurrence of various prey items was counted. Individuals were generally identified to order.

Table 2—Stomach contents of salmon and trout of differing ages and habitats in the Burrishoole catchment. Values are the number of fish stomachs which contained each taxa.

	Salmon					*Trout*				*Total*	*% occurrence*
Age	0+	1+	0+	1+	2+ (smolt)	0+	1+	0+	1+		
Habitat	littoral	littoral	river	river	pelagic	littoral	littoral	river	river		
n	7	10	5	5	24	12	10	6	5	84	
Diptera	3	10	3	1	16	5	8	5	5	56	67%
Ephemeroptera	5	8	0	0	3	7	6	2	1	32	38%
Plecoptera	3	3	2	4	2	6	7	2	2	31	37%
Trichoptera	0	7	3	2	6	0	3	1	4	26	31%
Coleoptera	0	2	4	2	0	3	5	2	3	21	25%
Daphnia	0	0	0	0	21	0	0	0	0	21	25%
Mollusca	0	7	1	2	0	0	1	0	1	12	14%
Amphipoda	1	0	0	0	0	2	3	0	0	6	7%
Bosmina	0	0	0	0	6	0	0	0	0	6	7%
Cyclopoid	0	0	0	0	5	0	0	0	0	5	6%
Hymenoptera	1	0	0	0	0	0	3	0	0	4	5%
Lepidoptera	1	0	0	0	0	1	1	0	0	3	4%

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All pre-weighed samples were analysed by the Colorado State Plateau Stable Isotope Laboratory at Northern Arizona University, using a Thermo-Electron Delta V Advantage IRMS configured through a Finnigan CONFLO III for automated continuous-flow analysis of $\delta^{15}N$ and $\delta^{13}C$, and a Carlo Erba NC2100 elemental analyser for combustion and separation of C and N. Stable isotope ratios were expressed in δ notations as parts per thousand (‰) using the following equation:

$$\delta X = [(R_{sample}/R_{standard})-1] \times 1000$$

The standard for carbon was the Vienna Pee Dee belemnite (VPDB) and atmospheric nitrogen (AIR) for nitrogen. NIST 1547 (peach leaves) was used as the internal laboratory working standard to check on measurement reproducibility throughout each run. The isotope correction standards used were IAEA CH6 and CH7 for $\delta^{13}C$, and IAEA N1 and N2 $\delta^{15}N$. The precision for this analysis run (calculated from the standard deviations for the NIST peach leaves) was ±0.09‰ for $\delta^{13}C$ and ± 0.08‰ for $\delta^{15}N$.

DATA ANALYSIS

The stomach contents of groups of fish were visualised using nMDS (following double square root transformation and calculation of Bray-Curtis dissimilarities) with the R package *vegan* (Oksanen *et al.* 2015) and analysed for differences between groups using the *adonis* function (analysis of variance using distance matrices) (McArdle and Anderson 2001). The input data for this analysis was the number of individuals of each taxon that were found in each fish stomach (Supplemental information II)

Following the recommendation of Post *et al.* (2007), animal samples with a C:N ratio >3.5 were lipid corrected, as lipids are depleted in $\delta^{13}C$, using the equation:

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} -3.3 + 0.99 \star C{:}N$$

Trophic position (TP) was estimated within each sampled habitat (river and lake) using either periphyton or a primary consumer as a baseline, using the equation:

$$TP_{consumer} = ([\delta^{15}N_{consumer} - \delta 15N_{baseline}]/3.23) + \lambda$$

where 3.23 ‰ is the trophic-enrichment factor taken from the literature, $\delta^{15}N$ baseline is the mean $\delta^{15}N$ value of the baseline resource of the system, and λ is the trophic position of the baseline resource (1 for periphyton, 2 for primary consumer) (Vander Zanden and Rasmussen 2001; Manetta, Benedito-Cecilio and Martinelli 2003; Dekar *et al.* 2011; Wieczorek *et al.* 2018).

We used mixing models with the SIAR package in R to determine the most likely dietary sources for river and lake fish and hence evaluate the production base supporting juvenile salmonids in both habitats. SIAR is a Bayesian mixed model that uses Markov Chain Monte Carlo simulations to determine the probable contribution to diet of different prey sources (Parnell *et al.*, 2008). We used consumer-based dual- isotope models ($\delta^{13}C$ and $\delta^{15}N$) for fish from each habitat, with the end members being the signatures of aquatic macroinvertebrates, adult flies and pelagic zooplankton. All sampled food sources were included in the lake model (both river and lake invertebrates) as theoretically, lake fish may only have been in the lake for a very short period of time and may still maintain a 'riverine' dietary signal. In contrast, we assume that fish caught in the rivers had never spent time in the lake, and so the end members for the river model were only those invertebrates sampled in the river (mayfly) and adult flies. We used trophic enrichment values of 0.91 ‰ ± 1.04 for $\delta^{13}C$ and 3.23 ‰ ± 0.41 for $\delta^{15}N$ (Dekar *et al.*, 2011).

RESULTS

STOMACH CONTENT ANALYSIS

We carried out stomach analysis on 84 fish as part of this study, and 12 different taxa were represented across all fish (Table 2). One individual each of Hymenoptera (ants) and Lepidoptera (moths and butterflies) were found in the stomachs of the river salmon – these were excluded from analysis owing to their rarity. Diptera (flies) were the most common food item found in the stomachs, with a mix of both terrestrial and aquatic life stages. 67% of fish had Diptera in their stomachs at the time of sampling, followed by Ephemeroptera (mayflies: 38%), Plecoptera (stoneflies: 37%) and Trichoptera (caddisflies: 31%). When all 84 fish were analysed together, there were significant differences in the stomach contents of the various groups of fish (*adonis*, p=0.001, F=6.13, n=84), the most notable difference being the diet of 2+ salmon (smolts migrating from the pelagic zone of Lough Feeagh) when compared with all other groups (Fig. 2). For fish sampled in the Lodge and Srahrevagh rivers, species was a significant source of variation in observed stomach contents (*adonis*, p=0.03, F=3.27, n=21), with trout stomachs containing relatively more Diptera, while salmon were eating more Plecoptera (Fig. i, Supplemental Information). Age class was not a significant source of variation in the diets of river fish, with large overlap between the food items of 0+ and 1+ fish. In contrast, in the littoral region of Lough Feeagh, the age of the fish (0+ vs 1+) was a more important discriminant of diet (*adonis*, p=0.009,

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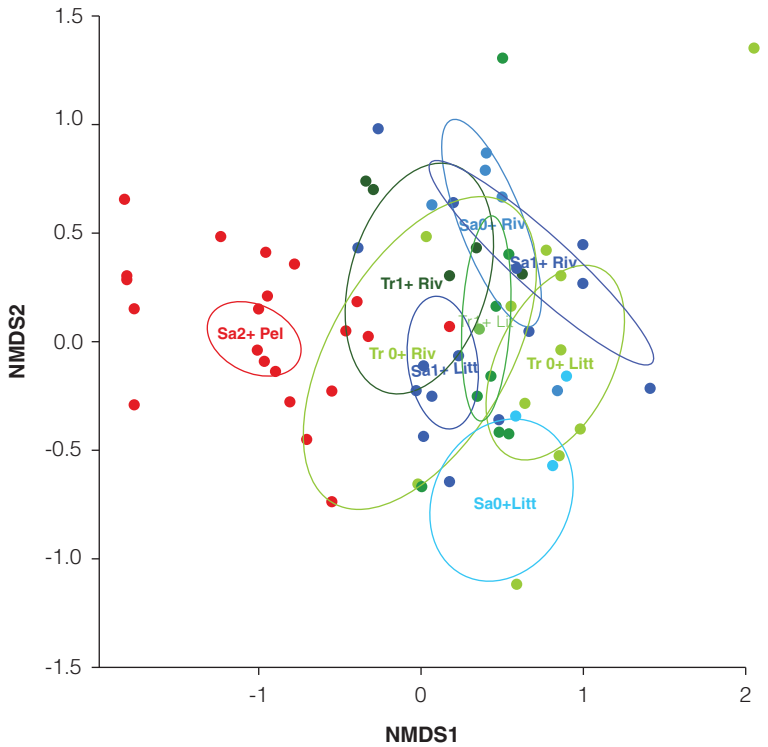


Figure 2—nMDS ordination of the stomach contents of salmon and trout sampled in the Burrishoole catchment from river and littoral lake habitats. Ellipses are plotted as the standard error of the (weighted) average of scores, and the grey lines indicate segments connecting each sample to the group centroid. Stress = 0.15, n= 84.

F=3.02, n=39) than the species (salmon vs trout), with the 0+ feeding more on Ephemeroptera and Plecoptera, and 1+ fish of both species feeding more on Trichoptera and Diptera (Fig. ii, S.I.).

In order to examine the changes in diet as fish aged, salmon and trout were also analysed separately. There was a difference between the stomach contents of the pelagic salmon smolts (2+) and the 0+ and 1+ salmon from river and lake littoral habitats (*adonis*, $p<0.001$, F=14.77, n=49) (Fig. iii, S.I.). The smolts were eating mainly zooplankton, predominantly *Daphnia* sp., with an average number of 200 individual *Daphnia* per smolt stomach. 21 out of 23 salmon smolts examined had large numbers of *Daphnia* in their stomachs. Two other zooplankton taxa, *Bosmina* sp. and cyclopoid copepods, were also found in the salmon smolt stomachs, along with Diptera and small numbers of EPT (Ephemeroptera, Plecoptera and Trichoptera). When analysed separately from the salmon smolts, there was some separation between the stomach contents of salmon sampled in rivers and those sampled in the lake littoral region (Fig. 3) (*adonis*, $p<0.001$, F=7.17, n=27). Coleoptera and Plecoptera were found more frequently in the river salmon, while the lake salmon had higher occurrences of molluscs. Ephemeroptera were not found in the stomachs of any salmon sampled in the rivers, although they were very common in the lake fish. While the diet of 0+ and 1+ river salmon overlap considerably, there was quite a divergence between 0+ and 1+ diets in the lake fish, with Trichoptera and Mollusca being absent from 0+ stomachs, but occurring in 70% of the 1+ stomachs.

Although there was more overlap in the stomach contents of trout than those of salmon described above, there were still some significant differences in the taxa found in the stomachs of lake trout compared to those of river trout (*adonis*, $p<0.01$, F=2.14, n=33) (Fig. 4). In particular, Amphipoda (*Gammarus duebenii*) were found in several lake trout, but not at all in river trout, while lake trout also had higher occurrences of Plecoptera and Ephemeroptera (Table 2). When amphipods were found in trout stomachs, it was in large numbers (17, 53 and 101 individuals in three fish)

STABLE ISOTOPE ANALYSIS

All the invertebrate samples (but not the fish) had a C:N ratio of >3.5, and so were lipid normalised. The $\delta^{13}C$ of samples ranged between -19.70‰ (lake periphyton) and -31.92‰ (conifer needles), and the $\delta^{15}N$ ranged between -3.26‰ (bog plants)

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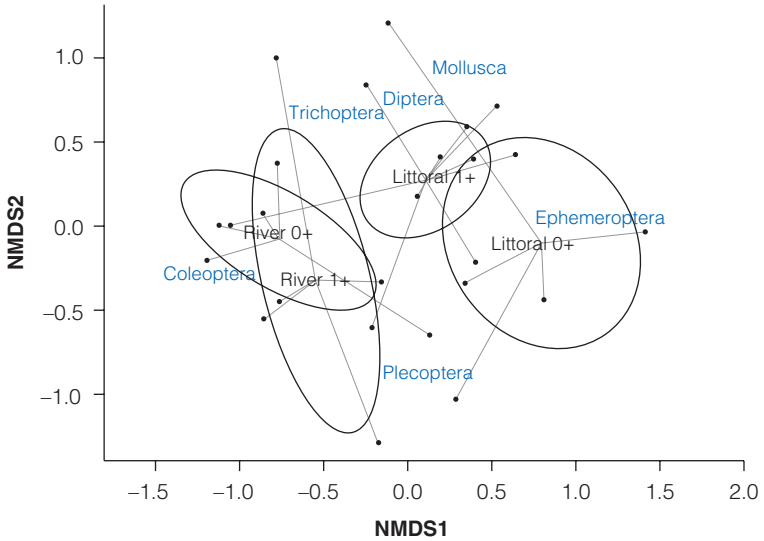


Figure 3—nMDS ordination of the stomach contents of salmon sampled in the Burrishoole catchment from river and littoral lake habitats (i.e. excluding smolts). Ellipses are plotted as the standard error of the (weighted) average of scores, and the grey lines indicate segments connecting each sample to the group centroid. Stress = 0.16, n= 27.

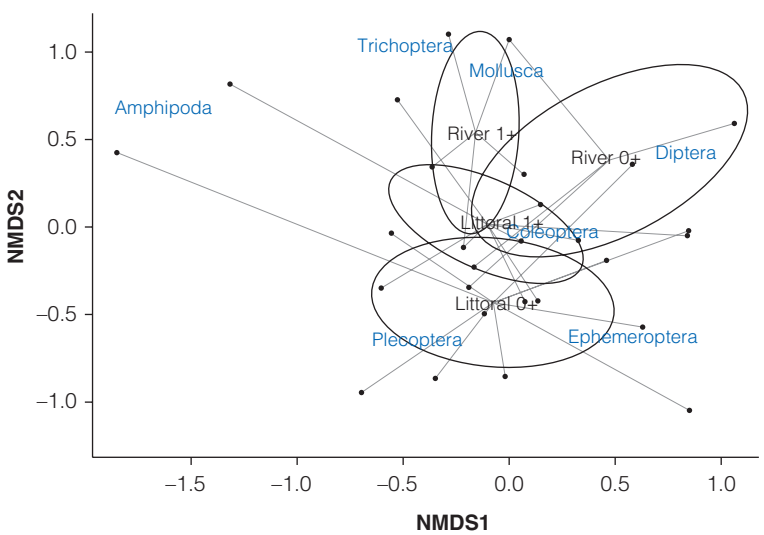


Figure 4—nMDS ordination of the stomach contents of trout sampled in the Burrishoole catchment from river and littoral lake habitats. Ellipses are plotted as the standard error of the (weighted) average of scores, and the grey lines indicate segments connecting each sample to the group centroid. Stress = 0.16, n= 27.

and 10.02‰ (Salmon 1+ lake) (Table 3). While the $\delta^{13}C$ of the lake periphyton seems to be an outlier in comparison to all other samples, it is within the range of other measurements in freshwater ecosystems (Jardine *et al.* 2003) and so we have included it in further analysis. The $\delta^{13}C$ measured in the fish ranged between -31.32 and -21.54, with fish becoming less depleted in $\delta^{13}C$ as they moved down the catchment from headwaters towards the sea. The dual isotope plots clearly show the trophic structure of the river and lake aquatic ecosystems in the catchment, with at least three trophic levels being characterised. Terrestrial primary producers (plants) are clearly separated at the base of the food web, with $\delta^{15}N$ values less than 0‰, while fish are grouped together at the top, with $\delta^{15}N$ between 8‰ and 10‰. In the middle of these two extremes are invertebrate consumers and a mix of periphyton, soils and sediments perhaps colonised with complex microbial assemblages (Fig. 5). The trophic position

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Table 3—Average stable isotope results from samples taken around the Burrishoole catchment in 2015/2016.

Sample	*n*	*δ13C ‰*	*δ13Cnorm‰*	*δ15N ‰*	*%C*	*%N*	*C:N*
Basal resources							
Peat Soil	5	-28.17		-0.07	59.50	2.45	24.37
Mineral soil	5	-27.77		3.51	12.15	0.50	22.50
Surficial Sediment	5	-28.59		3.55	13.18	0.82	16.29
Bog plants	5	-29.38		-3.26	49.72	1.16	42.92
Conifer Needles	5	-31.92		-1.84	49.04	1.16	42.18
Lake leaves	5	-31.76		-0.82	44.87	1.52	29.48
River Periphyton	5	-27.73		2.77	7.04	0.51	16.16
Lake Periphyton	4	-19.70		4.52	10.10	1.36	7.59
Invertebrates							
Adult DIptera	4	-31.50	-30.40	4.08	46.80	10.53	4.47
Mayflies (River)	3	-27.46	-24.58	4.82	51.54	8.27	6.27
Gammarids (lake)	3	-23.77	-22.69	7.02	35.75	8.06	4.44
Mayfly (lake)	5	-27.33	-26.64	8.38	48.66	12.03	4.05
Daphnia	3	-30.17	-27.50	7.34	33.29	5.79	6.05
Cyclopoid	3	-28.08	-26.22	9.64	46.35	8.84	5.23
Fish							
Trout 0+ (river)	6	-27.07		8.29	41.83	13.12	3.19
Salmon 1+ (river)	5	-27.65		8.50	42.31	13.06	3.24
Trout 0+ (lake)	17	-25.52		8.67	43.54	13.31	3.34
Salmon 0+ (river)	5	-28.96		8.76	40.98	12.68	3.23
Salmon 0+ (lake)	10	-26.18		8.92	42.78	12.78	3.35
Trout 1+ (river)	5	-27.08		9.03	40.00	12.47	3.21
Trout 1+ (lake)	10	-26.33		9.44	46.04	14.30	3.22
Salmon 2+ (smolt)	24	-24.62		9.67	42.58	13.61	3.14
Salmon 1+ (lake)	20	-24.15		10.02	44.82	13.72	3.27

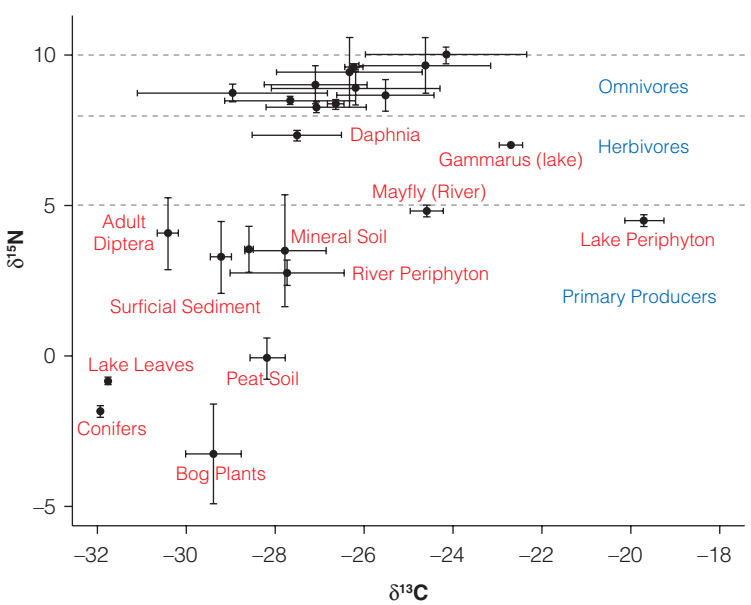


Figure 5—Dual isotope plot ($\delta^{13}C$ and $\delta^{15}N$) for basal resources, invertebrates (labelled) and fish (unlabelled – see Fig. 6) sampled in the Burrishoole catchment. Grey dashed lines indicate arbitrary ranges for trophic groups ($\delta^{15}N$) from Jardine et al. (Jardine *et al.*, 2003) and are for indicative purposes only. Error bars indicate one standard deviation.

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of lake primary producers, primary consumers and predators appears to be elevated in comparison to the same groups in rivers, indicating a more complex food web downstream in the catchment (Fig. 5). The $\delta^{15}N$ of river periphyton was 2.77‰, compared to 4.51‰ for lake periphyton. River mayflies (primary consumers) had a $\delta^{15}N$ of 4.82‰, while *Gammarus* in the littoral regions of Lough Feeagh had a $\delta^{15}N$ of 7.02‰. Interestingly, mayfly in Lough Feeagh appear to be feeding at more than one trophic position higher than the same family in river, with a $\delta^{15}N$ of 8.38‰, which was within the range of $\delta^{15}N$ measured in fish (Fig. 6). Similarly, cyclopoid copepods in Feeagh, which are generally considered to be primary consumers had an average $\delta^{15}N$ of 9.57‰, which was considerably higher than the other pelagic consumer, *Daphnia*, which had an average $\delta^{15}N$ value of 7.33‰.

If periphyton is used as the baseline for the aquatic food webs in Burrishoole's rivers and lakes, salmon and trout occupy a trophic position between 2 and 3, with a considerable range, particularly in lake fish (Fig. xi, S.I.). When a primary consumer is used as the baseline, with a trophic position of 2, there is a slight shift upwards in the trophic position of fish inhabiting the lake, but still occupying a range between 2 and 3. Lake mayfly appear to be feeding at the same trophic position as the 0+ trout and salmon. As we did not sample the true phytoplankton baseline that we would expect zooplankton to be feeding on, the trophic position of *Daphnia* and Cyclopoid copepods in Figure 7 should be treated with caution, but we note that cyclopoids do seem to be feeding at a slightly higher trophic level than their pelagic co-inhabitants *Daphnia*. In the river food web, using a primary consumer (a mix of mayfly species) as a baseline leads to estimated trophic positions of greater than three for all four fish groups (0+ and 1+ salmon and trout) (Fig. xi, S.I.).

A total of nine fish groups were sampled for stable isotope analysis (Table 3) and there was a large amount of overlap in the isotope signatures of these groups. The most enriched $\delta^{15}N$ was found in 1+ salmon sampled from the littoral area of Lough Feeagh, while 0+ river trout had the least. Interestingly, both cyclopoids and mayflies sampled in Lough Feeagh had SI ratios in the same range as those of fish. Although there is a lot of overlap in the SI signatures of the groups of fish, significant differences do appear between species, habitat and age class. $\delta^{15}N$ was less enriched in river fish when compared to lake fish (ANOVA, $p < 0.01$, $F = 21.5$), trout had significantly lower $\delta^{15}N$ than salmon (ANOVA, $p < 0.01$, $F = 14.0$) and fish became more enriched

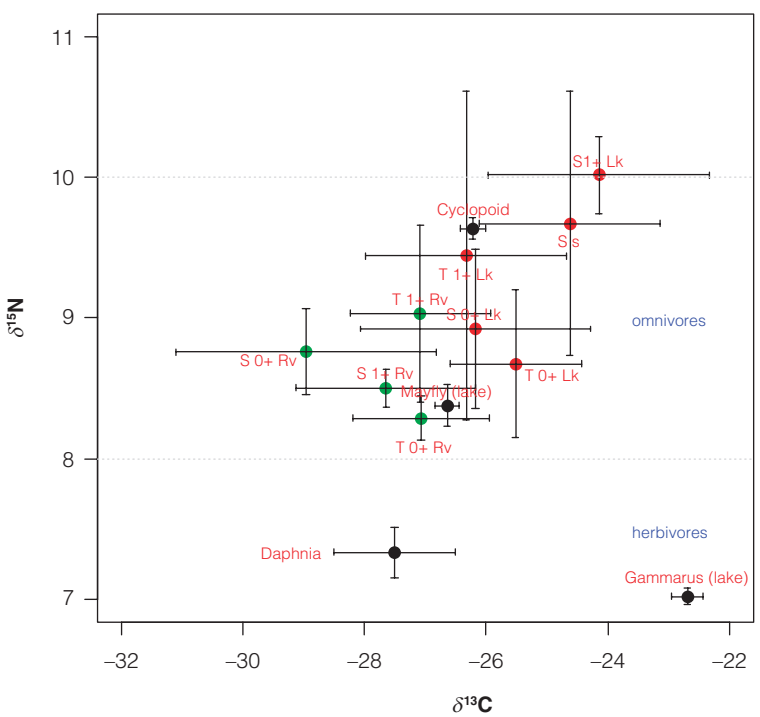


Figure 6—Dual isotope plot ($\delta^{13}C$ and $\delta^{15}N$) for invertebrates and fish (Salmon – S; Trout – T; 0+ and 1+ and s – 2+ smolt) sampled in the Burrishoole catchment. Grey dashed lines indicate arbitrary ranges for trophic groups ($\delta^{15}N$) from Jardine et al. (Jardine *et al.*, 2003) and are for indicative purposes only. Green circles are river fish (Rv), red are lake fish (Lk) and black are invertebrates for reference. Error bars indicate one standard deviation.

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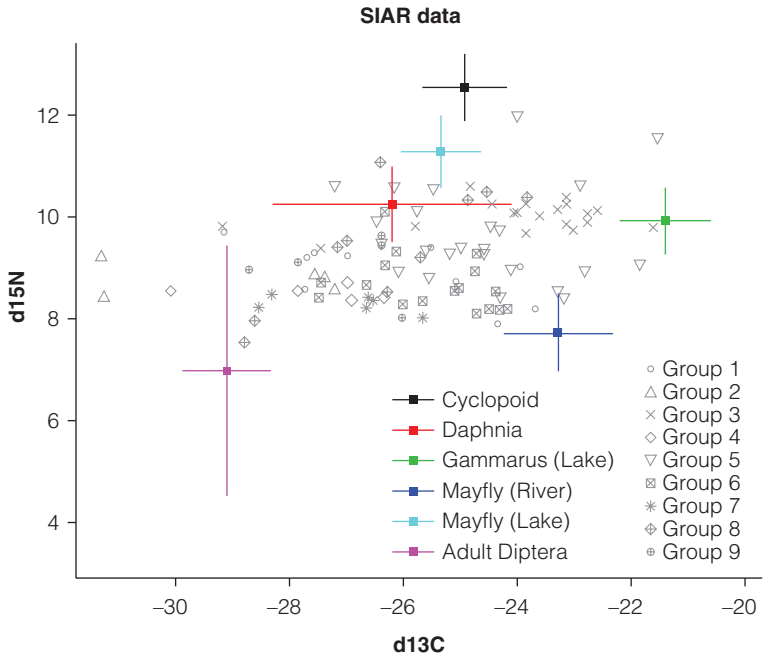


Figure 7—Raw isotope data for sources and consumers (lake fish) as a bi-plot. Trophic enrichment factors have been applied to the sources. Group 1 = Salmon 0+, group 2 = salmon 1+, group 3 = salmon smolts, group 4 = trout 0+ and group 5 = trout 1+.

in $\delta^{15}N$ as they grew from 0+ to 1+ (ANOVA, $p < 0.01$, $F = 11.2$). Although salmon smolts (2+) had higher $\delta^{15}N$ than 0+ salmon, it was actually lower than the $\delta^{15}N$ signature of 1+ lake salmon. $\delta^{13}C$ did not vary as much as $\delta^{15}N$ amongst groups, with the only significant difference being between habitat (ANOVA, $p < 0.01$, $F = 39$) where river fish were significantly depleted in $\delta^{13}C$ in comparison to lake fish. $\delta^{13}C$ did not vary with species or age class.

We used the R package SIAR to ascertain the likely food sources of groups of fish. In the isotopic $\delta^{15}N$ - $\delta^{13}C$ biplot, all lake fish fell within the area bounded by their prey items, all of which had been found during stomach content analysis (Fig 7). The results from the Bayesian model indicated varying prey items were important for each group of fish. Riverine mayflies and adult flies were the most important prey items for 0+ salmon sampled from the littoral region of the lake (S.I.). Riverine mayflies were also important in the diet of 1+ salmon in the lake, but adult flies were not. Instead, *Gammarus* made up approximately one third of the diet of these fish. Both riverine mayflies and *Gammarus* were also important components of smolt diets. It is of note that *Daphnia* did not appear, from the SIA, to be an important part of the diet of smolts migrating out of the lake, even though stomach content analysis of the same fish showed that *Daphnia* were the most numerous prey items at the time of capture, with the stomachs containing an average of 200 individuals.

The diet of 0+ lake trout was roughly similar to that of 0+ salmon, with riverine mayflies and adult flies making up approximately one third each of their diet. Finally, adult flies make up the biggest proportion of the diet of 1+ trout in Lough Feeagh, followed by riverine mayflies and *Daphnia*. The diet of 1+ trout is the only place where *Daphnia* appears to be somewhat important, indicating that perhaps these fish spend some time in the pelagic zone (S.I.).

The biplot of the river dwelling salmonids with their prey items indicates that we may have missed some important prey items when conducting our field sampling, as there were no prey items bounding the upper limit of the $\delta^{15}N$ range (Fig. 8). However, based on this initial analysis, the data indicate that mayflies and adult flies can contribute significant energy to salmonids in the rivers leading into Lough Feeagh. In particular, adult flies may constitute about 80% of the diet of 0+ salmon in the Srahrevagh and Lodge rivers (S.I.).

DISCUSSION

The food items found in the stomachs of salmon and trout in Burrishoole were generally as we would expect from literature. Salmonids in Ireland are known to feed primarily on both the larval and adult life stages of EPT taxa and Diptera (Frost 1938;

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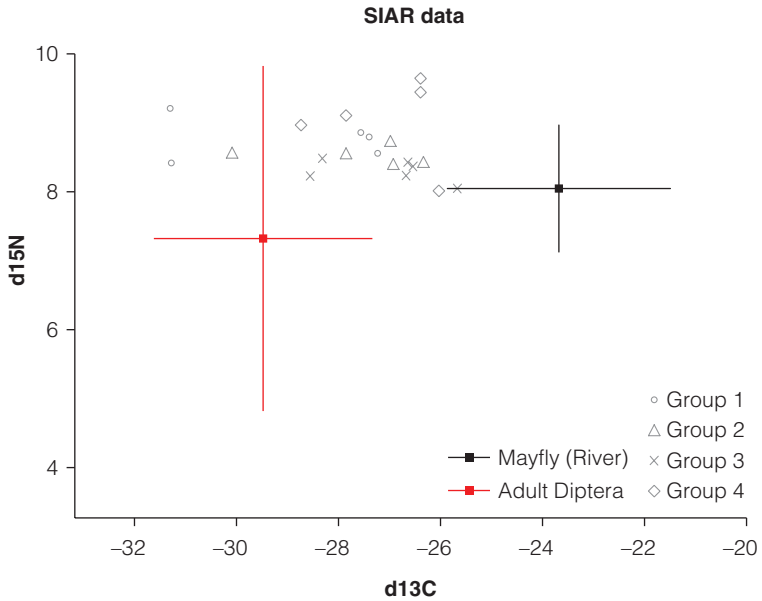


Figure 8—Raw isotope data for sources and consumers (river fish) as a bi-plot. Trophic enrichment factors have been applied to the sources. Group 1 = Salmon 0+, group 2 = salmon 1+, group 3 = trout 0+ and group 4 = trout 1+.

Stinson 1957; Lehane *et al.* 2001) and our results support this. While some studies report a considerable amount of molluscs and crustaceans in trout diets (Dauod, Bolger and Bracken 1986; Byrne, Poole and McGinnity 2000), we did not find this to be the case, with the exception of some *Gammarus* in five out of 33 trout sampled, all from the lake. This is probably a reflection of the acidic nature of the Burrishoole catchment and its underlying geology, which has low alkalinity, and low concentrations of base cations such as calcium. Occurrences of invertebrate taxa that require lots of calcium are therefore rare, apart from small pockets in Lough Feeagh and some of the rivers draining the east side of the catchment where there are veins of well buffered rocks. Previous studies have concluded that the importance of terrestrial insects becomes greater with increasing age of fish (Kelly-Quinn and Bracken 1990; Dineen, Harrison and Giller 2007), and this may account for some of the differences in stomach contents with age class in both salmon and trout in this study. However, the largest difference in diet, according to SCA, was associated with habitat. The stomach contents of lake and river dwelling fish of both species were significantly different, likely reflecting the differing availability of prey items in lentic and lotic habitats.

One surprising feature of the SCA was the predominance of *Daphnia* in the stomachs of salmon migrating through Lough Feeagh. Salmon can successfully feed and grow on a diet of Cladocera (Holm and Møller 1984), and some previous studies have reported *Daphnia* in the stomach contents of juvenile lake dwelling salmonids (Morrison 1983). However, we were unable to find much literature describing the binge-feeding that we observed in this study. According to the SIA results, both riverine mayflies and *Gammarus* were important components of the diet of salmon smolts, which seems counter-intuitive when compared with the SCA data which implied a predominantly pelagic lake diet. It may be that the smolts we sampled had come straight out of the upstream rivers into the lake, without spending enough time in the lake to accumulate a 'lake' diet signal. We note that it could take up to three months for the isotopic composition of new prey items to be detectable in consumers (Persson and Hansson 1999; Davis *et al.* 2018) and is more useful in assessing diets over weeks to months. Our combined SCA and SIA results indicate that even though smolts were feeding almost exclusively on *Daphnia* as they migrated through the lake, it was over a relatively short period of time, and most of their energy was previously derived from benthic invertebrates. It is currently unknown what proportion of Burrishoole smolts have spent the whole previous year in the lake (i.e. when they migrate permanently out of the upstream rivers into Lough Feeagh). However, these results imply that their migration time through the lake might only be a couple of days or weeks, rather than months. As we sampled the smolts over the whole migration period, we assume we sampled the variation in lake dwelling that occurs in Burrishoole salmon, and we conclude that salmon in this system generally use the lake habitat for only a very short period of time, immediately prior to their migration

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to sea. Sampling these smolts at a later stage may elucidate the contribution of this binging on *Daphnia* to their overall lifetime success. In general, *Daphnia* are present in Lough Feeagh around the same time as the smolt run (late spring into early summer), raising the question of what would happen in years where there is a mismatch between the smolt run and *Daphnia* bloom. One serious shortcoming of our study is that the SIA of *Daphnia* reported here was carried out on samples which were obtained several months prior to the smolt sampling (October 2015 vs May 2016), and it is quite likely that the SI signature of *Daphnia* in May is different from that obtained in October of the previous year. Previous analysis of the SI signature of *Daphnia* in Lough Feeagh displayed some seasonal variation, with $\delta^{13}C$ varying between -25.2‰ in October 2011 and -27.3‰ in May 2012, and $\delta^{15}N$ increasing from 6.7‰ to 7.8‰ (Ryder 2015). The results from this study measured -27.5‰ and 7.34‰, which were actually nearer to the values recorded in May 2012 than those of October 2011. We therefore conclude that the *Daphnia* signal used in our SIAR analysis gives a fair indication of the occurrence of *Daphnia* in smolt diet.

While SIA is not a new technique, studies of the stable isotope signatures of Irish salmon and trout are rather rare. We found reference to five other Irish studies (Table 4), some unpublished. Dineen (2005) measured $\delta^{13}C$ and $\delta^{15}N$ in salmon and trout from various rivers in North Mayo, including several in the Burrishoole catchment. $\delta^{15}N$ values in salmon were comparable to those reported here, ranging between 7.8‰ and 11.8‰. Our salmon results ranged between 8.5‰ and 10.0‰, indicting fish feeding at similar trophic levels in both studies. However, the $\delta^{15}N$ in trout reported in Dineen (2005) was slightly higher, indicting an additional trophic level in that study, possibly encompassing 2+ fish, or higher levels of nitrogen in the system. All the trout in our study were relatively small 0+ and 1+ fish and their $\delta^{15}N$ reflects this. Some of the larger values of $\delta^{15}N$ found across Ireland and Scotland (Table 4) can be partially attributed to the size of the fish (e.g. Keaveney, Reimer and Foy 2015), as trout become progressively more ^{15}N-enriched with fish length, particularly as they move to a more piscivorous diet (Grey 2001). When comparing $\delta^{15}N$ amongst fish from different systems however, it is important to note that one of the primary determinants of $\delta^{15}N$ will be the nutrient status of the aquatic habitat, and so any comparisons will be more informative when the baseline conditions are taken into account.

The range of $\delta^{13}C$ measured across Ireland is large, particularly for salmon, indicating large variation in the food sources of salmonids across the country. Even data from the most comparable study (Dineen 2005) indicated a slightly more enriched carbon signature than that recorded in this study, with values of -22‰ recorded in some rivers (in comparison to our highest value of -24.2‰). This may be owing to the inclusion of fish from more productive rivers in north Mayo, where significant biofilms can provide a source of nutrition. It may also be owing to the fact that sampling occurred slightly earlier in the year than in the present study, and we know that SI signatures can vary significantly with time (Syväranta, Hämäläinen and Jones 2006; Ryder 2015). Some of the very low values in $\delta^{13}C$ (e.g. salmon in the river Outeragh) can be attributed

Table 4—Average stable isotope signatures of juvenile salmon and trout in Irish and Scottish waterbodies.

	Country	*Species*	*δ13C ‰*	*δ15N ‰*	*Source*
This study	Ireland	Salmon	-28.9 to -24.2	8.5 to 10.0	
Mayo rivers	Ireland	Salmon	-29.8 to -22.0	7.8 to 11.8	(Dineen 2005)
Outeragh River	Ireland	Salmon	-39.2 to -35.3	9.4 to 10.7	(Graham *et al.* 2013)
Lough Neagh	Ireland	Salmon	-30.2 to -28.7	10.8 to 15.7	(Harrod unpublished)
River Inny	Ireland	Salmon	-33.4 to -27.7	11.8 to 15.0	(Maguire *et al.* 2011)
Upper Lough Corrib	Ireland	Salmon	-28.5 to -26.6	12.5 to 14.0	(Maguire *et al.* 2011)
This study	Ireland	Trout	-27.1 to -25.5	8.3 to 9.4	
Mayo rivers	Ireland	Trout	-29.3 to -22.4	8.4 to 11.0	(Dineen 2005)
River Awbeg	Ireland	Trout	-29.4 to -26.4	10.5 to 12.4	(Graham *et al.* 2013)
Lough Neagh	Ireland	Trout	-28.8 to -20.0	12.3 to 16.8	(Harrod unpublished)
River Inny	Ireland	Trout	-32.6 to -26.7	11.1 to 17.8	(Maguire *et al.* 2011)
Upper Lough Corrib	Ireland	Trout	-31.2 to -24.8	8.4 to 15.6	(Maguire *et al.* 2011)
Lough Erne	Ireland	Trout	-32.6 to -28.8	14.1 to 19.4	(Keaveney *et al.* 2015)
Lough Lomond	Scotland	Trout	-27.7 to -17.8	8.4 to 14.4	(Etheridge *et al.* 2008)
River Enrick	Scotland	Trout	-26.0 to -22.5	7.5 to 9.9	(Grey 2001)
Loch Ness	Scotland	Trout	-27.9 to -21.1	8.0 to 14.2	(Grey 2001)

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to the calcareous nature of the system, with possible fixation of methane by primary producers leading to depleted carbon isotope ratios (Graham, Harrison and Harrod, 2013).

The results from this study show that salmonids in Burrishoole are supported by a wide range of carbon energy sources, with the main split along the allochthony / autochthony gradient occurring as fish move downstream out of the headwater rivers and into Lough Feeagh. The shift in $\delta^{13}C$ between river and downstream lake habitats is consistent with the stream continuum concept whereby consumers are highly dependent on allochthonous carbon sources in headwaters, and that this dependence shifts more to autochthonous sources in downstream habitats (Doucett *et al.* 1996). This is not to say that allochthonous sources of energy in downstream lakes (e.g. lake litter) are not important, but rather that in-lake processing of organic matter and the addition of aquatic primary production (lake phytoplankton and phytobenthos) may lessen this importance. Determining the exact contribution of allochthonous and autochthonous sources to the diet of salmonids in Burrishoole was not possible with the data collected during this study, although the results presented here provide a very informative first step in designing a follow-up study with more targeted fieldwork. This might include trying to physically isolate phytoplankton and phytobenthic samples and hence accurately measure the baseline autochthonous isotopic signature required in models detecting the carbon source utilized in food web studies (Wilkinson *et al.* 2013; Keaveney *et al.* 2015).

The inclusion of allochthonous sources, and microbial processing of organic matter is likely to be the main reason for the range of trophic levels that we observed in the salmonid food web of Burrishoole. Primary producers (plants) are clearly separated at the base of the food web, with $\delta^{15}N$ values less than 0‰, while fish are grouped together at the top, with $\delta^{15}N$ between 8 and 10‰. In the middle of these two extremes are invertebrate consumers and a mix of periphyton, soils and sediments perhaps colonised with complex microbial assemblages. Using both periphyton and primary consumers as baselines for trophic position calculation placed salmonids somewhere between 2 and 3.5. Determination of trophic position is heavily influenced by the baseline $\delta^{15}N$ that is used (Anderson and Cabana, 2007), and it may be that either the periphyton or the primary consumers which we used as our baselines in both river and lake habitats were not the true baselines. In upstream rivers, we found a large gap in the trophic position between our baseline consumer (mayflies) and the fish, and it is likely that we missed some secondary consumers in this food chain. Lake periphyton may not truly represent the first trophic level of the lake food chain, as it may already have been colonised by a wide range of microinvertebrates and microbes. For example, had we used decomposing leaf litter as our baseline, salmonids would have been assigned to a trophic position greater than three. The wide range of observed trophic positions assigned to juvenile salmon and trout in Burrishoole is likely to be a consequence of omnivory, but differences in fractionation of nitrogen from one trophic level may also play a part (Jones and Waldron 2003). It also hints at food web complexity in both Lough Feeagh and the upstream rivers. Fish are functionally multi-chain omnivores, deriving energy from both periphyton- and phytoplankton-based food chains (Vadeboncoeur *et al.* 2005), as demonstrated by the wide range of $\delta^{13}C$ values recorded amongst fish cohorts (min=-31.3‰, max = -21.5‰), indicating wide utilisation of allochthonous and autochthonous sources.

The combination of stomach content analysis (SCA) and stable isotope analysis (SIA) is informative at several levels. For salmon, SCA indicated clear separation between the diets of fish from the three habitats: river, lake littoral and lake pelagic, and also a separation between the diet of 0+ and 1+ salmon in the lake littoral region. This distinction by habitat and/or age corresponded with a significant difference in $\delta^{13}C$ amongst salmon occupying the two habitats, and also manifested as a difference in $\delta^{15}N$ amongst groups. This change in $\delta^{15}N$ is consistent with fish changing their trophic position with habitat and age, perhaps as they grow larger, and are able to eat larger prey items. Although separation was less obvious in the trout samples examined for SCA, there was some differentiation between the diets of river and lake fish, but not between trout of different ages.

According to the SIA, 1+ trout are the only cohort apart from the salmon smolts where *Daphnia* appears to be somewhat important, indicating that perhaps these fish spend some time in the pelagic zone. The suggestion from this analysis is that riverine mayflies are a more likely source of energy to lake fish than mayfly living in the lake. This is rather surprising, but perhaps understandable when we look at the position of these lake mayflies in the isotope biplots (Fig. 6), where they are situated very close to the 0+ lake fish. It is possible that these lake mayflies are too big for juvenile salmonids to eat (they were all large *Heptagenia* sp. individuals), and we may have missed characterising smaller mayfly for this analysis. In contrast, the riverine mayfly samples comprise a mix of three species, including the smaller *Baetis rhodani*, which is probably a more palatable prey item for these small fish. Had we known the results from the stomach content analysis before we carried out the fieldwork, we would have paid more attention to characterising the prey items found in the river fish. For example, we decided to collect mayfly in the rivers as a signal of aquatic invertebrates, but these were not actually

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found in the stomachs of the river salmon. Inclusion of some Trichoptera or Plecoptera might have given us more accurate end-members for the Bayesian mixing model conducted with SIAR. Similarly, the fact that riverine mayflies appear to be important in the diet of lake fish indicates either that the lake fish were moving in and out of areas in the lakes where smaller mayflies (with a riverine signal) were available for consumption, or alternatively, that we missed sampling an important portion of the food web that matches the SI signature of riverine mayflies. Nevertheless, the SCA and SIA both confirm the reliance of many salmonids on adult flies as a source of energy. The two analyses also show that there is clear separation between age classes and species as fish move between different habitats. The combination of SCA and SIA also highlights the swift binging of the smolts on zooplankton as they move downstream through Lough Feeagh to the sea, and indicates that this may be a very short lived, but likely important, phenomenon. The SIA has allowed us to construct a first draft of the food web supporting salmonids in Burrishoole, and this will support future research on determining how changes in land use and climate may affect different trophic levels, and hence fish production.

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REFERENCES

Allott, N., McGinnity, P. and O'Hea, B. 2005 Factors influencing the downstream transport of sediment in the Lough Feeagh catchment, Burrishoole, Co. Mayo, Ireland. *Freshwater Forum* **23**, 126–38.

Anderson, C. and Cabana, G. 2007 Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes. *Journal of the North American Benthological Society* **26**, 273–85. https://doi.org/10.1899/0887–3593(2007)26[273:ETTPOA]2.0.CO;2

Asmala, E., Carstensen, J. and Räike, A. 2019 Multiple anthropogenic drivers behind upward trends in organic carbon concentrations in boreal rivers. *Environmental Research Letters* **14**, 124018. https://doi.org/10.1088/1748–9326/ab4fa9

Bartels, P., Cucherousset, J., Steger, K., Eklöv, P., Tranvik, L.J. and Hillebrand, H. 2012 Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* **93**, 1173–82. https://doi.org/10.1890/11–1210.1

Blenckner, T., Adrian, R., Livingstone, D.M., Jennings, E., Weyhenmeyer, G.A., George, D.G., *et al.* 2007 Large-scale climatic signatures in lakes across Europe: a meta-analysis. *Global Change Biology* **13**, 1314–26. https://doi.org/10.1111/j.1365–2486.2007.01364.x

Bonn, A., Allott, T., Hubacek, K. and Stewart, J. 2009 Managing change in the uplands - challenges in shaping the future. In: *Drivers of environmental change in uplands* (Eds A. Bonn, T. Allott, K. Hubacek and J. Stewart), 475–94. Routledge, London and New York.

Byrne, C., Poole, R. and McGinnity, P. 2000 Food consumed by wild and stocked brown trout, Salmo trutta L., and salmon, Salmo salar L., in an Irish lake. *SIL Proceedings, 1922–2010* **27**, 185–88. https://doi.org/10.1080/03680770.1998.11901223

Couture, S., Houle, D. and Gagnon, C. 2012 Increases of dissolved organic carbon in temperate and boreal lakes in Quebec, Canada. *Environmental Science and Pollution Research* **19**, 361–71. https://doi.org/10.1007/s11356–011–0565–6

Dalton, C., O'Dwyer, B., Taylor, D., de Eyto, E., Jennings, E., Chen, G., *et al.* 2014 Anthropocene environmental change in an internationally important oligotrophic catchment on the Atlantic seaboard of western Europe. *Anthropocene* **5**, 9–21. https://doi.org/10.1016/j.ancene.2014.06.003

Dauod, H.A., Bolger, T. and Bracken, J.J. 1986 Age, Growth and Diet of the brown trout Salmo Trutta L. in the Roundwood Reservoir System

Davis, M.J., Woo, I., Ellings, C.S., Hodgson, S., Beauchamp, D.A., Nakai, G., *et al.* 2018 Integrated Diet Analyses Reveal Contrasting Trophic Niches for Wild and Hatchery Juvenile Chinook Salmon in a Large River Delta. *Transactions of the American Fisheries Society* **147**, 818–41. https://doi.org/10.1002/tafs.10088

Dekar, M.P., King, R.S., Back, J.A., Whigham, D.F. and Walker, C.M. 2011 Allochthonous inputs from grass-dominated wetlands support juvenile salmonids in headwater streams: evidence from stable isotopes of carbon, hydrogen, and nitrogen. *Freshwater Science* **31**, 121–32. https://doi.org/10.1899/11–016.1

Dineen, G. 2005 *Terrestrial Energy Subsidies for Salmonids*. University College Cork, Cork.

Dineen, G., Harrison, S.S.C. and Giller, P.S. 2007 Diet partitioning in sympatric Atlantic salmon and brown trout in streams with contrasting riparian vegetation. *Journal of Fish Biology* **71**, 17–38. https://doi.org/10.1111/j.1095–8649.2007.01441.x

Doucett, R.R., Power, G., Barton, D.R., Drimmie, R.J. and Cunjak, R.A. 1996 Stable isotope analysis of nutrient pathways leading to Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 2058–66. https://doi.org/10.1139/f96–132

Doyle B.C., Eyto E. de, Dillane M., Poole R., McCarthy V., Ryder E., *et al.* 2019 Synchrony in catchment

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stream colour levels is driven by both local and regional climate. *Biogeosciences* **16**, 1053–71. https://doi.org/10.5194/bg-16–1053–2019

Etheridge, E.C., Harrod, C., Bean, C. and Adams, C.E. 2008 Continuous variation in the pattern of marine v. freshwater foraging in brown trout Salmo trutta L. from Loch Lomond, Scotland. *Journal of Fish Biology* **73**, 44–53. https://doi.org/10.1111/j.1095–8649.2008.01905.x

de Eyto, E., Dalton, C., Dillane, M., Jennings, E., McGinnity, P., O'Dwyer, B., *et al.* 2016a The response of North Atlantic diadromous fish to multiple stressors, including land use change: a multidecadal study. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1759–69. https://doi.org/10.1139/cjfas-2015–0450

de Eyto, E., Jennings, E., Ryder, E., Sparber, K., Dillane, M., Dalton, C., *et al.* 2016b Response of a humic lake ecosystem to an extreme precipitation event: physical, chemical and biological implications. *Inland Waters* **6**, 483–98. https://doi.org/10.1080/IW-6.4.875

Fealy, R., Allott, N., Broderick, C., de Eyto, E., Dillane, M., Erdil, R.M., *et al.* 2014 *RESCALE: Review and Simulate Climate and Catchment Responses at Burrishoole*. Galway.

Finstad, A.G., Helland, I.P., Ugedal, O., Hesthagen, T. and Hessen, D.O. 2014, Unimodal response of fish yield to dissolved organic carbon. *Ecology letters* **17**, 36–43

Freeman, C., Evan, C.D., T.M.D., Reynolds, B. and Fenner, N. 2001 Export of organic carbon from peat soils. *Nature* **412**, 785

Frost W.E. 1938 River Liffey Survey: II. The Food Consumed by the Brown Trout (Salmo trutta Linn.) in Acid and Alkaline Waters. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science* **45**, 139–206

Gallego-Sala, A.V., Clark, J.M., House, J.I., Orr, H.G., Prentice, I.C., Smith, P., *et al.* 2010 Bioclimatic envelope model of climate change impacts on blanket peatland distribution in Great Britain. *Climate Research* **45**, 151–62. https://doi.org/10.3354/cr00911

Graham, C.T., Harrison, S.S.C. and Harrod, C. 2013 Development of non-lethal sampling of carbon and nitrogen stable isotope ratios in salmonids: effects of lipid and inorganic components of fins. *Isotopes in Environmental and Health Studies* **49**, 555–66. https://doi.org/10.1080/10256016.2013.808635

Grey, J. 2001 Ontogeny and dietary specialization in brown trout (Salmo trutta L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen. *Ecology of Freshwater Fish* **10**, 168–76. https://doi.org/10.1034/j.1600–0633.2001.100306.x

Holm, J. Chr. and Møller, D. 1984 Growth and prey selection by Atlantic salmon yearlings reared on live freshwater zooplankton. *Aquaculture* **43**, 401–12. https://doi.org/10.1016/0044–8486(84)90248–5

Ise, T., Dunn, A.L., Wofsy, S.C. and Moorcroft, P.R. 2008 High sensitivity of peat decomposition to climate change through water-table feedback. *Nature* **1**, 763–66

Jardine, T.D., McGeachy, S.A., Paton, C.M., Savoie, M. and Cunjak, R.A. 2003 Stable isotopes in aquatic systems: Sample preparation, analysis, and interpretation. *Can. Manuscr. Rep. Fish. Aquat. Sci.* **2656**, 1–39

Jennings, E., Allott, N., McGinnity, P., Poole, R., Quirke, W., Twomey, H., *et al.* 2000 The North Atlantic Oscillation: Effects on Freshwater Systems in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* **100B**, 149–57

Jennings, E., Jarvinen, M., Allott, N., Arvola, L., Moore, K., Naden, P., *et al.* 2010 Impacts of climate on the flux of dissolved organic carbon from catchments. In: *The Impact of Climate Change on European Lakes*. Aquatic Ecology Series, (Ed. G. George), 199–20. Springer, London.

Jones, J.I. and Waldron, S. 2003 Combined stable isotope and gut contents analysis of food webs in plant-dominated, shallow lakes. *Freshwater Biology* **48**, 1396–407. https://doi.org/10.1046/j.1365–2427.2003.01095.x

Jones, M.B., Donnelly, A. and Albanito, F. 2006 Responses of Irish vegetation to future climate change. *Biology and Environment: Proceedings of the Royal Irish Academy* **106B**, 323–34

Karlsson, J., Berggren, M., Ask, J., Byström, P., Jonsson, A., Laudon, H., *et al.* 2012 Terrestrial organic matter support of lake food webs: Evidence from lake metabolism and stable hydrogen isotopes of consumers. *Limnology and Oceanography* **57**, 1042–48. https://doi.org/10.4319/lo.2012.57.4.1042

Keaveney, E.M., Reimer, P.J. and Foy, R.H. 2015 Young, Old, and Weathered Carbon—Part 2: Using Radiocarbon and Stable Isotopes to Identify Terrestrial Carbon Support of the Food Web in an Alkaline, Humic Lake. *Radiocarbon* **57**, 425–38

Kelly-Quinn, M. and Bracken, J.J. 1990 A seasonal analysis of the diet and feeding dynamics of brown trout, Salmo trutta L., in a small nursery stream. *Aquaculture Research* **21**, 107–24. https://doi.org/10.1111/j.1365–2109.1990.tb00386.x

Layer, K., Hildrew, A.G., Jenkins, G.B., Riede, J.O., Rossiter, S.J., Townsend, C.R., *et al.* 2011 Chapter Two - Long-Term Dynamics of a Well-Characterised Food Web: Four Decades of Acidification and Recovery in the Broadstone Stream Model System. In: *Advances in Ecological Research*. (Ed. G. Woodward), pp. 69–117. Academic Press.

Lehane, B.M., Walsh, B., Giller, P.S. and O'Halloran, J. 2001 The influence of small-scale variation in habitat on winter trout distribution and diet in an afforested catchment. *Aquatic Ecology* **35**, 61–71. https://doi.org/10.1023/A:1011467711628

Maguire, C., Gallagher, K., Maggs, C., Dick, J., Caffrey, J.M., O'Flynn, C., *et al.* 2011 *Alien Invasive Species in Irish Water Bodies*. EPA report 2007-W-MS-2-S1. Wexford.

Manetta, G.I., Benedito-Cecilio, E. and Martinelli, M. 2003 Carbon sources and trophic position of the main species of fishes of Baía River, Paraná River floodplain, Brazil. *Brazilian Journal of Biology* **63**, 283–90. https://doi.org/10.1590/S1519–69842003000200013

McArdle B.H. and Anderson M.J. 2001 Fitting Multivariate Models to Community Data: A Comment on Distance-Based Redundancy Analysis. *Ecology* **82**, 290–97. https://doi.org/10.1890/0012–9658(2001)082[0290:FMMTCD]2.0.CO;2

McGinnity, P., Jennings, E., de Eyto, E., Allott, N., Samuelsson, P., Rogan, G., *et al.* 2009 Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased

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risk of climate-mediated extinction. *Proceedings of the Royal Society of London B: Biological Sciences* **283**, 3601–10

Meyers, P.A. 2003 Applications of organic geochemistry to paleolimnological reconstructions: a summary of examples from the Laurentian Great Lakes. *Organic Geochemistry* **34**, 261–89. https://doi.org/10.1016/S0146–6380(02)00168–7

Morrison, B.R.S. 1983 Observations on the food of juvenile Atlantic salmon, Salmo salar L, reared in a Scottish hill loch. *Journal of Fish Biology* **23**, 305–13. https://doi.org/10.1111/j.1095–8649.1983.tb02909.x

O'Gorman, R., Lantry, B.F. and Schneider, C.P. 2004 Effect of Stock Size, Climate, Predation, and Trophic Status on Recruitment of Alewives in Lake Ontario, 1978–2000. *Transactions of the American Fisheries Society* **133**, 855–67. https://doi.org/10.1577/T03–016.1

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., *et al*. 2015 *vegan: Community Ecology Package. R package version 2.2–1.*

Parnell, A., Inger, R., Bearhop, S. and Jackson, A. 2008 SIAR: stable isotope analysis in R. *The Comprehensive R Archive Network) Available at http://cran.r-project.org/web/packages/siar/index.html* [Verified 15 July 2012]

Persson, A. and Hansson, L.-A. 1999 Diet shift in fish following competitive release. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 70–78. https://doi.org/10.1139/f98–141

Poole, W.R., Dillane, M., de Eyto, E., Rogan, G., McGinnity, P. and Whelan, K. (2006). Characteristics of the Burrishoole Sea Trout Population: Census, Marine Survival, Enhancement and Stock-Recruitment Relationship, 1971–2003. In: *Sea Trout: Biology, Conservation and Management* (Eds G. Harris and N. Milner), pp. 279–306. Blackwell, Oxford.

Poole, W.R., Diserud, O.H., Thorstad, E.B., Durif, C.M., Dolan, C., Sandlund, O.T., *et al.* 2018 Long-term variation in numbers and biomass of silver eels being produced in two European river systems. *ICES Journal of Marine Science*. https://doi.org/10.1093/icesjms/fsy053

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J. and Montaña, C.G. 2007 Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**, 179–89. https://doi.org/10.1007/s00442–006–0630-x

Renou-Wilson, F., Bolger, T., Bullock, C., Convery, F., Curry, J., Ward, S., *et al.* 2011 BOGLAND: Sustainable Management of Peatlands in Ireland. *STRIVE Report Series*, 181

Ryder, E. 2015 *Estimating Carbon Pools and Processing in a Humic Lake*. Dundalk Institute of Technology, Dundalk.

Ryder, E., de Eyto, E., Dillane, M., Poole, R. and Jennings, E. 2014 Identifying the role of environmental drivers in organic carbon export from a forested peat catchment. *Science of The Total Environment* **490**, 28–36. https://doi.org/10.1016/j.scitotenv.2014.04.091

Solomon, C.T., Carpenter, S.R., Clayton, M.K., Cole, J.J., Coloso, J.J., Pace, M.L., *et al.* 2011 Terrestrial, benthic, and pelagic resource use in lakes: results from a three-isotope Bayesian mixing model. *Ecology* **92**, 1115–25. https://doi.org/10.1890/10–1185.1

Sparber, K. 2012 *Neo- and palaeolimnological investigations in a humic and a clear water lake in the west of Ireland*. Mary Immaculate College, University of Limerick.

Stinson, N.E. 1957 The Food and Growth of Brown Trout (Salmo trutta L.) in Three Rivers in Co. Tyrone. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science* **59**, 129–54

Syväranta, J., Hämäläinen, H. and Jones, R.I. 2006 Within-lake variability in carbon and nitrogen stable isotope signatures. *Freshwater Biology* **51**, 1090–02. https://doi.org/10.1111/j.1365–2427.2006.01557.x

Tanentzap, A.J., Szkokan-Emilson, E.J., Kielstra, B.W., Arts, M.T., Yan, N.D. and Gunn, J.M. 2014 Forests fuel fish growth in freshwater deltas. *Nature Communications* **5**, 4077. https://doi.org/10.1038/ncomms5077

Trueman, C.N., Johnston, G., O'Hea, B. and MacKenzie, K.M. 2014 Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140669

Vadeboncoeur, Y., McCann, K.S., Zanden, M.J.V. and Rasmussen, J.B. 2005 Effects of Multi-chain Omnivory on the Strength of Trophic Control in Lakes. *Ecosystems* **8**, 682–93. https://doi.org/10.1007/s10021–003–0149–5

Vander Zanden, M.J. and Rasmussen, J.B. 2001 Variation in δ15N and δ13C trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography* **46**, 2061–66. https://doi.org/10.4319/lo.2001.46.8.2061

Wieczorek, A.M., Power, A.M., Browne, P. and Graham, C.T. (2018). Stable-isotope analysis reveals the importance of soft-bodied prey in the diet of lesser spotted dogfish Scyliorhinus canicula. *Journal of Fish Biology* **93**, 685–93. https://doi.org/10.1111/jfb.13770

Wilkinson, G.M., Carpenter, S.R., Cole, J.J., Pace, M.L. and Yang, C. 2013 Terrestrial support of pelagic consumers: patterns and variability revealed by a multilake study. *Freshwater Biology* **58**, 2037–49. https://doi.org/10.1111/fwb.12189

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